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UNIVERSITY OF ALBERTA

A CHEMOSYSTEMATIC STUDY OF *KALMIA* L. (*ERICACEAE*) USING FLAVONOID CHARACTERS

BY

SHUNGUO LIU ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN
PLANT TAXONOMY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
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Dr. Keith E. Denford ....
Dr. Randall J. Bayer ....Randall J Bayer.......
Co-supervisors

Dr. Mark R.T. Dale ....Mark R.T. Dale.......
Dr. George E. Ball ....Geo E Ball.......
Dr. Randolph S. Currah ....Randolph Currah.......
Dr. John Bain .......J.F. Bain.......
External Examiner

Date ..16 June 1993.....

Dedication

To my family

Abstract

Kalmia (*Ericaceae*), a genus of shrubs (rarely small trees) endemic to North America and Cuba, has extraordinarily rich flavonoids. A total of 85 flavonoids involving nine flavonoid types have been isolated from the genus, and 76 of them were isolated from the present study. Of the 76 flavonoids isolated, 61 of them are the first reports from *Kalmia*. A total of 53 flavonoids were identified or partially identified with the remaining 23 of them being tentatively characterized to flavonoid types.

The present study attempts to reevaluate the systematic relationships among *Kalmia* species using flavonoids as characters, since there exist different treatments of the genus. The flavonoid profiles of 248 populations from all *Kalmia* taxa were analyzed using multivariate statistics. The results of both cluster analyses and principal component analyses generally support treatment of *Kalmia* species by J.E. Ebinger (Rhodora 76: 351-398, 1974) with minor differences. The present study recognizes all seven species recognized by Ebinger, namely: *Kalmia angustifolia* L., *K. cuneata* Michaux, *K. ericoides* Wright ex Griseb., *K. hirsuta* Walt., *K. latifolia* L., *K. microphylla* (Hook.) Heller, and *K. polifolia* Wang. Four varieties involving two species are recognized, 1) *Kalmia angustifolia* L. var. *angustifolia* and *K. angustifolia* L. var. *carolina* (Small) Fern. and 2) *Kalmia ericoides* Wright ex Griseb. var. *ericoides* and *K. ericoides* var. *aggregata* (Small) Ebinger. The proposed separation of *K. microphylla* (Hook.) Heller var. *microphylla* and *K. microphylla* (Hook.) Heller var. *occidentalis* (Small) Ebinger is rejected in favour of a single variable species with two chemotypes: chemotype "occidentalis" which is characterized by having an unidentified aurone #1 and dihydrochalcones; and chemotype "microphylla" without the two flavonoid types.

There is no strong correlation between the flavonoid profile and the structural features in *K. microphylla*, but the geographical distribution of chemotype "occidentalis" appears to be related to the extent of the Wisconsin glaciation. *Kalmia microphylla* var. *occidentalis* in the Pacific lowland area from Washington to Alaska, is distinctly separated from *Kalmia polifolia* by the present study.

The present study also provides a general taxonomic treatment of the species of *Kalmia*, as well as conclusions about relationships of the genus to other taxa of the *Ericaceae*.

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I. Introduction

A. Family *Ericaceae*

The family *Ericaceae* consists mainly of shrubs or small trees most of which are evergreen, but a few are deciduous (Cronquist 1981; Heywood 1978; Hutchinson 1973). Although the family is well known and has been recognized since the very start of the "family" concept (A.L. de Jussieu 1789), the circumscription of the family varies, ranging from 50 genera and 1350 species to 125 genera and 4000 species (Luteyn *et al.* 1980; Oliver 1991). The most recent estimate is 2245 species (Thorne 1992). The *Ericaceae* is cosmopolitan in distribution with three distribution centers being recognized by Stevens (1970a), i.e. southeast Asia, south/southeast Africa, and the Andes of South America.

There have been two attempts in recent years to classify the family at levels higher than genus (Watson *et al.* 1967; Stevens 1971). Stevens' classification of the family has been used by many authors. Stevens (1971) recognized six subfamilies, *Rhododendroideae* (7 tribes), *Ericoideae* (2 tribes), *Vaccinioideae* (5 tribes), *Pyroloideae*, *Monotropoideae*, and *Wittsteinioideae*, with about 100 genera and some 3000 species. Wallace (1975a, 1975b) studied the subfamily *Monotropoideae* and reinvestigated the relationships of the subfamilies of the *Ericaceae* and Stevens' (1971) treatment was accepted. Thorne's (1992) most recent classification of angiosperms also accepted Stevens's treatment. Steenis (1984) removed the genus (also the subfamily) *Wittsteinia* from the *Ericaceae* and placed it in the family *Alseuosmiaceae*, which, according to Oliver (1991), was also acknowledged by Stevens. With the advancement of new technologies and a better understanding of the family, the classification of the family is likely to be refined further with time. The recent paper by Cullings and Bruns (1992) confirmed the placement of *Monotropoideae* in *Ericaceae* while placing *Pyroloideae* into an independent family, *Pyrolaceae*. Cladistic analysis of the group also indicates a closer relationship between *Ericaceae* and *Monotropaceae* than either of them with *Pyrolaceae* (Anderberg 1992). However, the analysis offers only one synapomorphy (presence of andromedotoxins) in *Ericaceae* and *Monotropaceae*, separating them from *Pyrolaceae*, whereas there are five characters separating *Ericaceae* from *Monotropaceae*. Therefore the result (Anderberg 1992) is open to other taxonomic interpretations. Additional cladistic analyses indicate that the *Ericaceae*, as presently circumscribed, is paraphyletic, and that *Epacridaceae* and *Empetraceae* are better treated as members of the *Ericaceae* (Anderberg 1993; Judd and Kron 1993).

B. Tribe *Phyllodoceae* (*Rhododendroideae*)

Stevens (1971) recognized eight genera in this tribe: *Kalmia* L., *Kalmiopsis* Rehd., *Rhodothamnus* Reichenb., *Phyllodoce* Salisb., *Bryanthus* D. Don, *Loiseleuria* Meissn., *Leiophyllum* Hedwig F., and *Ledothamnus* Desv. The genera *Kalmiopsis*, *Rhodothamnus*, *Bryanthus*, *Loiseleuria*, and *Leiophyllum* are all monobasic and all have restricted distributions, except *Loiseleuria* which is circumpolar (Copeland 1943; Gleason 1951; Henderson 1931; Ohwi 1965; Peck 1961; Rehder 1932; Strand and Wyatt 1991; Tutin *et al.* 1972; Wilbur and Racine 1971; Wood 1961). *Ledothamnus* is the only genus in the tribe known from the Southern Hemisphere. Taxa of this genus are restricted to the Guyana Highland of Venezuela and Guyana (Maguire *et al.* 1978). Nine species were recognized in the genus (Copeland 1943; Gleason 1931; Gleason and Killip 1939; Maguire 1970; Maguire *et al.* 1978; Willis 1966). *Phyllodoce* has a Northern circumpolar and temperate distribution with at least seven species being recognized along with several hybrids (Abrams 1951; Britton and Brown 1931; Copeland 1943; Hitchcock *et al.* 1959; Hultén 1968; Jepson 1925; Ma 1980; Ohwi 1965; Scoggan 1979; Tutin *et al.* 1972; White and Johnson 1980).

The phylogenetic relationships among the eight genera are not well understood. Copeland (1943) regarded *Kalmia*, *Rhodothamnus* (including *Kalmiopsis*) and *Phyllodoce* as "primitive" genera within the tribe. Cox (1948) proposed three monophyletic clades within the tribe (note: he included *Diplarche*): 1) *Kalmia* and *Rhodothamnus* (*Kalmiopsis* was also included in this genus); 2) *Phyllodoce*, *Diplarche* and *Bryanthus*; 3) *Loiseleuria*, *Leiophyllum*, and *Ledothamnus*. Stevens (1971) considered *Kalmia* to have close relationships with *Phyllodoce*, *Rhodothamnus*, *Kalmiopsis*, and probably *Bryanthus*. He regarded *Loiseleuria* and *Leiophyllum* as a pair and *Ledothamnus* as a separate clade (also see Stevens 1970a). My own observations and analyses of the tribe in the light of morphology and flavonoid data (unpublished) indicate that *Kalmia* is rather closely related to *Loiseleuria* and *Leiophyllum*. *Bryanthus* is closely related to *Phyllodoce*. *Rhodothamnus* and *Kalmiopsis* are so similar in flavonoid profile that an unification of the two might be justified (Copeland 1943; Cox 1948). It has already been shown that the two genera can hybridize and produce seeds (Starling 1985)(note: the seeds are not viable; J.G. Packer, personal communication, 1993). Apparently both *Rhodothamnus* and *Kalmiopsis* are very closely related to *Phyllodoce*. *Rhodothamnus* can hybridize with *Phyllodoce* (Rehder 1951; Stevens 1970a). According to Dr. John G. Packer (personal communication 1993) who contacted Starling recently, one very interesting cross was made between *Phyllodoce breweri* and *Kalmiopsis leachiana*, and the hybrids can produce viable seeds. Morphologically *Phyllodoce breweri* has revolute leaves (versus ericoid) and somewhat open saucer-shaped (versus urceolate) corolla, and these features are shared by *Kalmiopsis leachiana*. In my view, *Kalmiopsis* or *Rhodothamnus* could have been the ancestor of *Phyllodoce*. *Ledothamnus* shows a quite distinct flavonol glycoside profile, and its ability to make triglycosides of quercetin, kaempferol, and myricetin distances itself from any genus in the tribe. The genus has been thought to have close affinities to the South African genus *Erica* based on their striking similarity of leaf structures (Camp 1947; Hagerup 1953; Maguire 1970). As Stevens (1970a) noted: "*Ledothamnus* is so different from *Ericoideae* in flower, fruit, and in stem anatomy that considering these characters alone, it is hard to see how the possibility of a relationship between them was ever suggested, but they are so similar in leaf that it is difficult to see how they could fail to be related." The placement of *Ledothamnus* in the *Ericaceae* should be reexamined. To conclude, *Ledothamnus* should be removed from the tribe and the remaining seven genera could form two closely related groups: 1) *Kalmia*, *Loiseleuria*, and *Leiophyllum*; and 2) *Kalmiopsis*, *Rhodothamnus*, *Phyllodoce*, and *Bryanthus*.

C. Genus *Kalmia*

Kalmia was named in commemoration of Peter (Pehr) Kalm (March 1716 - December 16, 1779), a Finnish-born botanist, a traveller, and a student of Linnaeus. Peter Kalm was educated at the universities of Åbo and Uppsala (Barnhart 1965; Stafleu and Cowan 1979; Anonymous 1981). He was sent to America by the Swedish Academy of Sciences, on the recommendation of Linnaeus, to obtain seeds of economically important plants and specifically to find a mulberry tree that would endure the severity of the Swedish climate for an independent silk industry (Benson 1937). Kalm came to

America in September 1748 and collected specimens in the New World (Pennsylvania, New York, New Jersey, and southern Canada) until his return in February 1751. *Kalmia latifolia* L. and *K. angustifolia* L. were among his collections. Upon his return to Europe in 1751, Kalm turned some of his collections over to Linnaeus. One of Linneaus' students, Leonhard Chenon, studied part of the collection and a new genus *Kalmia*, among others, was named in his "Nova Plantarum Genera" (1751). Both *K. latifolia* and *K. angustifolia* were named and described in Chenon's doctoral thesis (1751) and later were included in Linnaeus' (1753) "Species Plantarum" (see Holmes 1956). According to Juel and Harshberger (1929), in "Species Plantarum" Linneaus (1753) described 700 North American plants and in 90 cases he mentioned Kalm as the collector of the species, of which 60 were new (see Juel and Harshberger 1929, for a list of Kalm's plant collections deposited at the Botanical Museum in Uppsala).

Although *Kalmia* is a clearly defined genus, two other generic names were applied to this group of plants after 1753 (see Linnaeus 1753; Holmes 1956 for other pre-Linnaeus names). (1), The pre-Linnean name, *Chamaedaphne* Catesby, was used by Kuntze (1891) as a senior synonym of *Kalmia*. (2), Small (1903) segregated *Kalmia hirsuta* and placed it in the genus *Kalmiella*. The Cuban species *Kalmia ericoides* was later transferred to *Kalmiella* and a new Cuban species, *Kalmiella aggregata* was named (Small 1914). This treatment did not receive wide recognition, but was adopted by Britton (1920), Roig and Acuña (1957), Borhidi (1985), and Borhidi and Muñiz (1986). None of the recent revisions of *Kalmia* have adopted Small's treatments (Berazain & Sorribes 1987; Ebinger 1974; Judd 1983; Southall and Hardin 1974; Wood 1961). Anatomical and embryological studies do not support this separation (Copeland 1943; Cox 1948; Ganapathy and Palser 1964). Crossing experiments also show that *Kalmia* *hirsuta* is closely related to other *Kalmia* species and that there are no compelling reasons to separate it from *Kalmia* (Jaynes 1968a).

Kalmia which is generally considered to comprise a group of evergreen or deciduous shrubs (rarely trees), consists of six to ten species (Ebinger 1974, 1988a; Southall and Hardin 1974; Wood 1961). The genus is distributed in North America and Cuba, with most species occurring along the Appalachian Mountains (Fig. 1).

D. Economic Importance of *Kalmia*

The beautiful flowers of *Kalmia* have attracted many horticulturists and stimulated many studies beneficial to the understanding of the genus. Therefore a brief introduction regarding the economic importance of *Kalmia* is provided.

Kalmia is economically important as an ornamental, with the most important species being *K. latifolia* and *K. angustifolia* (Terrell *et al.* 1986). Several *Kalmia* species have been introduced to Europe for cultivation, including *K. latifolia* in 1734, *K. angustifolia* in 1736, *K. polifolia* in 1767, *K. cuneata* in 1820, and *K. hirsuta* in 1786 (Loudon 1842). *Kalmia latifolia* is a shrub and can also occur as a tree, and is listed as such in a number of publications (Sargent 1893, 1922; Britton 1908; Little 1979; Elias 1980; and Preston 1989; just to name a few). *Kalmia latifolia* was noted by Peter Kalm as being used for decorations in churches at Christmas or New Year (Benson 1937). Cultivars of *K. latifolia* were being named by 1840, and at present at least 90 names have been applied to different forms of the species (Rehder 1951; Ebinger 1974; Jaynes 1988a, 1988b). *Kalmia angustifolia* is another commonly cultivated species.

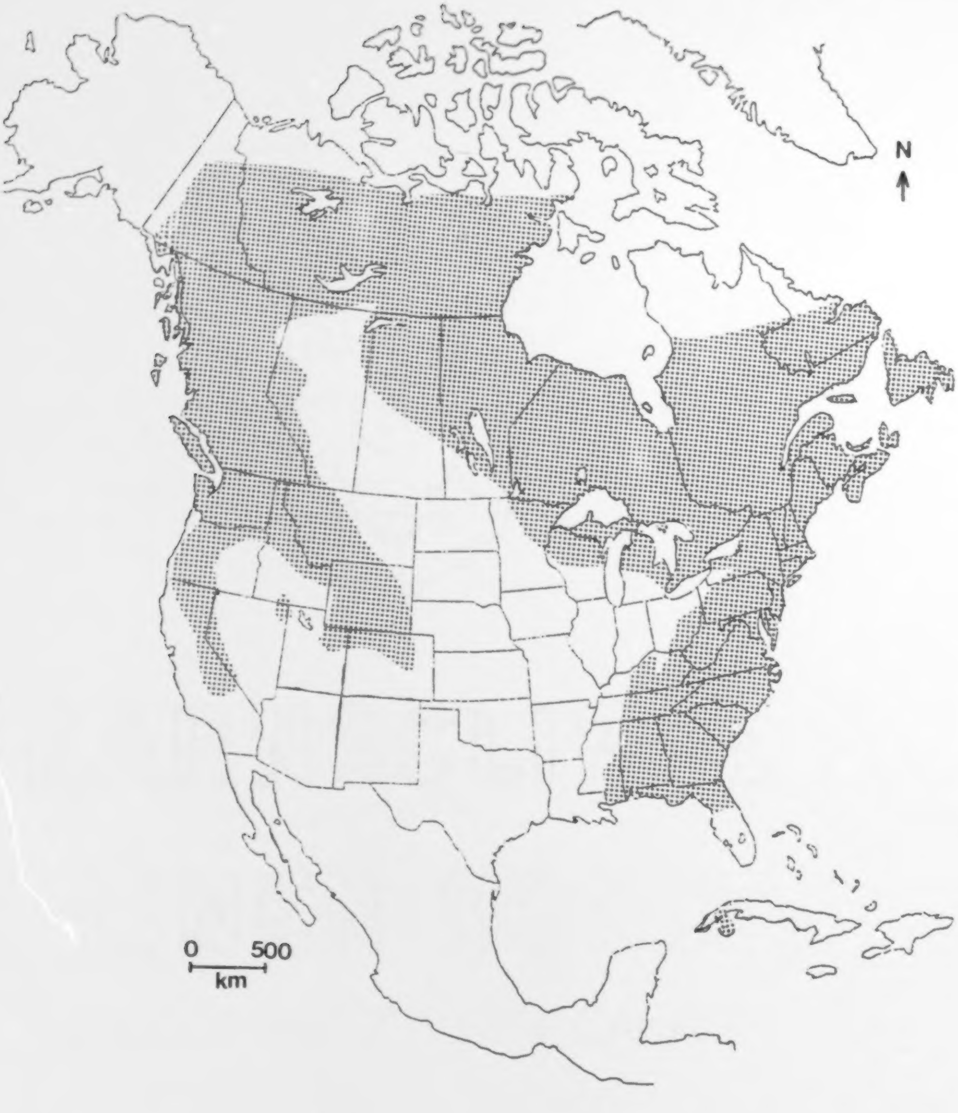

Figure 1. Distribution of *Kalmia* L. in North America and Cuba.

Kalmia is well-known as a weed in plantations of commercial shrubs such as blueberries and of timber trees. *Kalmia angustifolia* is difficult and sometimes costly to control in the blueberry fields (may cost $15-17/hectare for chemical control) and it is on the Canadian weed list (Hall *et al.* 1973; Ismail and Yarborough 1981). Recently it has been shown that *K. angustifolia* has allelopathic effects on black spruce seedling (*Picea mariana*), and has a competitive advantage over such trees. *Kalmia angustifolia* may have the same effects on balsam fir (*Abies balsamea*) or at least can play a role in reducing the growth of that tree (Thompson and Mallik 1989). Efforts at "weed control" of *Kalmia* are underway (Jobidon 1991; Mallik 1987, 1990, 1991, 1993; Mallik and Newton 1988; Peterson 1965).

The poisonous properties of *Kalmia* have been widely recorded since the early Nineteenth century (Barton 1802; Benson 1937; Ebinger 1974, 1988b; Griffith 1847, 1848; Muenscher 1940, 1960; Nuttall 1818; Pammel 1911). Common names of *K. angustifolia*, include lambkill, sheepkill, calfkill, all of which are indicative of its toxicity. It is also known that *K. latifolia*, *K. microphylla*, *K. polifolia* are poisonous (Clawson 1933; Dayton 1931; Ebinger 1988b; Kingsbury 1964; Marsh and Clawson 1930). The poisonous compound was identified as grayanotoxin I (andromedotoxin or acetyl-andromedol), a diterpene, which is also common in other ericaceous plants, such as *Rhododendron*, *Pieris*, *Lyonia*, and *Chamaedaphne* (Ebinger 1988b; Mancini and Edwards 1979). Over the past ten years, Professor Raymond W. Doskotch and co-workers at the College of Pharmacy, Ohio State University have been working on isolating and characterizing grayanoid diterpenes in *Kalmia*. So far they have completed *K. latifolia* and *K. angustifolia*, and more than ten grayanoid diterpenes have been isolated from the two species (El-Naggar and Doskotch *et al.* 1980; Burke *et* *al.* 1989; Burke and Doskotch 1990). Current work is underway on other species of *Kalmia* (Dr. Doskotch, July 1992, personal communication).

Kalmia has been used for medicinal purposes, e.g. *K. latifolia* as a cure for diarrhoea and itching, the leaf powder as snuff, and *K. hirsuta* as a cure for itching and mange in dogs (Ebinger 1988b). According to Ebinger (1988b), Professor J.M. Edwards *et al.* at School of Pharmacy, University of Connecticut have found an active, anti-cancer compound in the sap of *K. latifolia*. The structure of the compound is currently under investigation. These properties make *Kalmia* an important plant for other pharmaceutical products (Heisey and Gorham 1992).

E. History of Classification of the species of *Kalmia*

The most recent and detailed account on the history of *Kalmia* classification is that of Ebinger (1974; also see Southall and Hardin 1974). Since *K. latifolia* and *K. angustifolia* have been cultivated for a long time, many names have originated from horticulture (Ebinger 1974). The present study considers only those names frequently used in the taxonomic works in the current century.

Small (1933) recognized two assemblages of *Kalmia* (having excluded *Kalmiella*), *latifoliae* and *angustifoliae*. The former contains *K. latifolia* and the latter includes *K. angustifolia*, *K. carolina*, and *K. cuneata*. He did not indicate the rank of the two "groups", therefore the treatment is considered invalid (Greuter *et al.* 1988; Dale Vitt 1992, personal communication). Such grouping is not needed in a relatively small genus, so it will not be considered here. The subsequent discussions use the species delimitations from Ebinger (1974). A comparative treatment of all *Kalmia* species is summarized in Table 1.

Kalmia latifolia and *K. angustifolia* were included in Species Plantarum (Linnaeus 1753). *Kalmia latifolia* has been treated as a single species ever since. Although many names have been applied to it due to its long horticultural history, none of them were treated above the rank of form by Ebinger (1974) or have not been recognized at all (Southall and Hardin 1974).

Individuals of *Kalmia angustifolia* are evergreen shrubs with phyllotaxy of whorled leaves unique in the genus. Many horticultural names have been applied to horticultural forms of *K. angustifolia* (Ebinger 1974). Pursh (1814) described a variety *ovata* of the species based on the plants from the New Jersey mountains (no specimen mentioned). He described the plant as "*foliis latioribus subovatis, caule altiore*". The name was not recognized widely and faded into obscurity because the characters used are within the natural range of variation of the species (Ebinger 1974). Complications arose when Small (1903) published the species *K. carolina* based on a specimen collected at Flat Rock, North Carolina. The key he used to separate the two is as follows:

Leaf-blades glabrous, at least at maturity: style
  glabrous. *K. angustifolia*
Leaf-blades permanently canescent-tomentulose, at least
  beneath: style pubescent. *K. carolina*

This key did not work well, as in the treatment of 1933, Small used another key to separate the two:

Leaf-blades green, and dull above: pedicels and calyx
  usually glandular: corolla crimson or purplish.
  K. angustifolia
Leaf-blades glaucous above and shining: pedicels and calyx
  not glandular: corolla pink or white. *K. carolina*

Table 1. Comparison of Recent Treatments of *Kalmia*[1]

Southall & Hardin(1974)	Ebinger(1974)	Present Study
K. angustifolia	*K. ang*[2] var. *ang*	*K. ang* var. *ang*
K. carolina	*K. ang* var. *car*	*K. ang* var. *car*
K. cuneata	*K. cuneata*	*K. cuneata*
K. ericoides	*K. eri* var. *eri*	*K. eri* var. *eri*
K. simulata	*K. eri* var. *eri*	*K. eri* var. *agg*
K. aggregata	*K. eri* var. *agg*	*K. eri* var. *agg*
K. hirsuta	*K. hirsuta*	*K. hirsuta*
K. latifolia	*K. latifolia*	*K. latifolia*
K. microphylla		
Alpine or high latitude	*K. mic* var. *mic*	*K. microphylla*
Lower elevation	*K. mic* var. *occidentalis*	*K. microphylla*
K. polifolia		
Pacific lowland[3]	*K. mic* var. *occi*	*K. microphylla*
Eastern	*K. polifolia*	*K. polifolia*

Notes:

1. For more detailed treatments of *K. angustifolia - carolina*, *K. microphylla - polifolia*, *K. ericoides - simulata - aggregata*, see Tables 2-4.
2. *agg = aggregata; ang = angustifolia; car = carolina; eri = ericoides; mic = microphylla; occi = occidentalis.*
3. Pacific lowland is referred to the coastal area from Washington to Alaska; "Eastern" covers the area east of eastern Alberta.

The only clearly diagnostic character to separate them seems to be the presence or absence of glandular trichomes on pedicels and calyx. The fact is that even the holotype of *K. carolina* (NY!) designated by Small possesses a few glandular trichomes on its pedicels and calyx (Ebinger 1974; my own observation). Fernald (1937) regarded this southern entity as a variety of *K. angustifolia*. The treatments after 1937 were divided and no agreement was reached in the two most recent studies (Ebinger 1974; Southall and Hardin 1974). Ebinger followed Fernald's treatment, while Southall and Hardin accepted Small's (see Table 2 for a summary). Ebinger (1974) also acknowledged that "more studies are needed to clarify the status of these taxa" (p. 377).

Kalmia hirsuta Walt. and *K. cuneata* Michaux were named in 1788 and 1803 respectively. *Kalmia hirsuta* is a small, evergreen shrub commonly less than 30 cm high, distributed in the southeast corner of South Carolina, Georgia, Florida and Alabama. *Kalmia cuneata* is also a shrub and is separated from the rest of *Kalmia* by having deciduous leaves. It is restricted to North and South Carolina. Both species are taxonomically stable.

Kalmia polifolia Wang. and *K. microphylla* (Hook.) Heller are closely related: both are small, evergreen bog shrubs with shiny leathery decussate leaves. In the late 18th century, the cultivated plant introduced from Newfoundland was named *K. polifolia* by Wangenheim (1788; cf. Stafleu and Cowan 1988 for publication date) and *Kalmia glauca* by Aiton (1789). In the 19th century the name *K. glauca* was used by many authors, with *K. polifolia* being treated as a heterotypic synonym. *Kalmia polifolia* Wang. has priority. The confusion started when Hooker (1834) proposed three varieties within the species, var. *glauca*, var. *rosmarinifolia*, and var. *microphylla*. The variety

Table 2. Comparison of Treatments of the *Kalmia angustifolia-carolina* Complex by Various Botanists

Botanist(s)	*angustifolia* variant	*carolina* variant
Small(1903,14 & 33)	*K. ang*	*K. car*
Robinson & Fernald (1908)	*K. ang*	*K. car*
Britton & Brown (1913)	*K. ang*	*K. car*
Fernald (1937, 50 & 70)	*K. ang* var. *ang*	*K. ang* var. *car*
Copeland(1943)	*K. ang*	*K. car*
Rehder(1951)	*K. ang*	*K. car*
Gleason(1952)	*K. ang* var. *ang*	*K. ang* var. *car*
Wood(1961)	*K. ang* var. *ang*	*K. ang* var. *car*
Gleason & Cronquist (1963 & 91)	*K. ang* var. *ang*	*K. ang* var. *car*
Radford *et al.* (1968)	*K. ang* var. *ang*	*K. ang* var. *car*
Ebinger(1974)	*K. ang* var. *ang*	*K. ang* var. *car*
Southall & Hardin(1974)	*K. ang*	*K. car*
Present Study	*K. ang* var. *ang*	*K. ang* var. *car*

Note: *ang* = *angustifolia*; *car* = *carolina*.

microphylla was based on a specimen collected by Drummond in "swamps in the Rocky Mountains" and is clearly a high altitude entity corresponding to Ebinger's *K. microphylla* var. *microphylla*. The other two varieties were described as being found in eastern North America and rarely in Pacific low swampy grounds. The eastern North American entities correspond to Ebinger's *K. polifolia* while the Pacific lowland plants to *K. microphylla* var. *occidentalis* (Small) Ebinger. Heller (1898) considered the alpine entity entirely distinct from *K. glauca* and accorded it specific rank. The status of the Pacific lowland (it covers an area from Washington to Alaska in this study) entity has been a puzzle. In 1914, Small proposed the name *K. occidentalis*, based on a specimen collected in the foothills of Mt. Rainier, Washington, by Mrs. Bailey Willis. He regarded the Pacific lowland plants as being distinct from the typical eastern *K. polifolia* and the alpine entity, *K. microphylla*. His key for separating the three species is as follows:

Capsule spheroidal; calyx half as long as the capsule or more.
  Corolla less than 1.5 cm. wide; calyx 5-6.5 mm. wide; leaf-blades typically less than twice as long as wide. *K. microphylla*.
  Corolla more than 1.5 cm. wide; calyx 8-10 mm. wide; leaf-blades typically more than twice as long as wide. *K. occidentalis*.
Capsule ovoid-spheroidal or globose; calyx less than half as long as the capsule. *K. polifolia*.

This treatment by Small obviously did not convince many taxonomists working with the genus. Modern treatments of the two entities, *K. microphylla* and *K. occidentalis*, proposed by Small (1914) are summarized in Table 3. The entity *K. polifolia* is excluded from the table because for all the entries it was treated as an intact entity whether as a

Table 3. Comparison of Treatments of Western North American *Kalmia* by Various Botanists

Botanist(s)	Alpine or High Latitude Entity	Intermediate Entity	Pacific Coast Lowland Entity
Piper(1906)	*K. glauca* *mic*	---------	*K. glauca*
Rydberg (1906 & 22)	*K. mic*	---------	---------
Robinson & Fernald(1908)	*K. pol*	*K. pol*	*K. pol*
Hall(1912)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Britton & Brown(1913)	*K. pol*	*K. pol*	*K. pol*
Small(1914)	*K. mic*	*K. occi*	*K. occi*
Piper & Beattie(1915)	*K. pol* *mic*	---------	*K. pol*
Smiley (1921)	*K. pol* var. *mic*	---------	---------
Jepson(1925)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Tidstrom (1925)	*K. mic*	---------	---------
Benson(1930)	*K. mic*	---------	---------
Kirkwood (1930)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Copeland (1943)	*K. pol* var. *mic*	*K. pol* var. *mic*	*K. pol* var. *mic*
Hultén(1945)	*K. mic*	*K. pol*	*K. pol*
Fernald (1950 & 70)	*K. pol*	*K. pol*	*K. pol*
Abrams(1951)	*K. mic*	*K. pol* ssp. *occi*	*K. pol* ssp. *occi*

Table 3 continued

Davis(1952)	*K. pol* var. *mic*	---------	---------
Gleason(1952)	*K. pol*	*K. pol*	*K. pol*
Harrington (1954 & 64)	*K. pol* var. *mic*	---------	---------
Hitchcock *et al.*(1959)	*K. pol* var.*mic*	"intergrade"	*K. pol* var. *pol*
Peck(1961)	*K. pol* var. *mic*	*K. pol*	*K. pol*
Gleason & Cronquist (1963 & 91)	---------	---------	*K. pol*
Calder & Taylor (1965 & 68)	*K. pol* ssp. *mic*	---------	*K. pol* ssp. *pol*
Weber (1967)	*K. pol*	---------	---------
Boivin(1968)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Hultén(1968)	*K. pol* ssp. *mic*	---------	*K. pol* ssp. *pol*
Hitchcock & Cronquist(1973)	*K. mic*	*K. occi*	*K. occi*
Munz & Keck (1973)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Ebinger (1974)	*K. mic* var. *mic*	*K. mic* var. *occi*	*K. mic* var. *occi*
Southall & Hardin(1974)	*K. mic*	*K. mic*	*K. pol*
Welsh(1974)	*K. pol* var. *mic*	*K. pol* var. *pol*	*K. pol* var. *pol*
Gilkey & Dennis(1975)	*K. pol* var. *mic*	---------	*K. pol*

Table 3 continued

Dorn(1977)	*K. mic*	---------	--------
Taylor & MacBryde(1978)	*K. mic* ssp.*mic*	*K. mic* ssp. *occi*	*K. mic* ssp. *occi*
Scoggan (1979)	*K. pol* var. *mic*	---------	*K. pol* var. *pol*
Kartesz & Kartesz(1980)	*K. mic* var. *mic*	*K. mic* var. *occi*	*K. mic* var. *occi*
Layser(1980)	*K. pol*	---------	---------
Porsild & Cody(1980)	*K. pol* ssp. *mic*	*K. pol* ssp. *pol*	*K. pol* ssp. *pol*
White & Johnson(1980)	*K. mic*	---------	---------
Kuijt(1982)	*K. pol* ssp. *mic*	---------	---------
Soper & Heimburger(1982)	*K. pol*	*K. pol*	*K. pol*
Moss(1983)	*K. mic*	---------	*K. pol*
Riley(1984)	*K. mic*	---------	---------
Hinds(1986)	---------	---------	*K. pol*
Albee *et al.* (1988)	*K. pol*	---------	---------
Shaw(1989)	*K. pol*	---------	---------
Meidinger (1990)	*K. mic* ssp. *mic*	*K. mic* ssp. *occi*	*K. mic* ssp. *occi*
Wallace(1993)	*K. pol* ssp. *mic*	*K. pol* ssp. *pol*	*K. pol* ssp. *pol*
Present Study	*K. mic*	*K. mic*	*K. mic*

Note: *mic* = *microphylla*; *occi* = *occidentalis*;
pol = *polifolia*; ----: Not treated.

species or as a subspecific entity (variety or subspecies). There are several entries in Table 3 that are deduced from the context, especially from the distribution descriptions in given treatments. For example, Table 3 includes the treatment by Gleason and Cronquist (1991) which involves *K. polifolia* only. This is because the distribution description in it states: "Bogs; Lab. to **Alas.**, s. to n. N.J., Mich., Minn., and **Calif.**", in which I surmise that they regarded the Pacific lowland entity *K. occidentalis* as the same as *K. polifolia*. The two recent studies diverged widely over the treatment of *K. occidentalis*. Ebinger (1974) placed it as a variety of *K. microphylla* based on cytology ($2n=24$, the same as the high altitude entity), a qualitative character - absence of leaf midrib glands (present in eastern *K. polifolia*), and a quantitative character - seed length. Southall and Hardin (1974) considered it the same as eastern *K. polifolia* based on morphology and anatomy (Tables 1 & 3). Consequently, floristic works since 1974 have shown almost the same amount of disagreement as those written earlier (see Table 3). In the most recent treatment of Californian *Kalmia*, Wallace (1993) stated: "more study needed to clarify status of ssp. *microphylla*, sometimes considered a sp.".

The Cuban *Kalmia* are distributed discontinuously on the Isle of Pines, and Piñar del Rio, main island Cuba (Judd 1983; Berazain and Sorribes 1987, Fig. 16). They display a great deal of variation in height and pubescence. The first species described was *K. ericoides* Wright ex Griseb. in 1866 based on a specimen from Piñar del Rio. Small (1914) named a second Cuban species *K. aggregata* (under the generic name *Kalmiella*) based on a specimen from the Isle of Pines collected by Jennings (#324). Britton (1920) added a third species, *Kalmia simulata* (*Kalmiella simulata*), whose type was from the Isle of Pines (Britton & Wilson 14205). Wood (1961) regarded all three entities as a single species

Kalmia ericoides. On the other hand, Southall and Hardin (1974) recognized the three entities as distinct species. Ebinger (1974) considered them as a single species with two varieties, var. *ericoides* which has no or less pubescence found on the main island of Cuba (some populations on the Isle of Pines), and var. *aggregata* which is densely pubescent and restricted to the Isle of Pines. Judd (1983) reinvestigated the complex and separated them geographically, *Kalmia ericoides* var. *ericoides* on the main island, and *K. ericoides* var. *aggregata* on the Isle of Pines. Berazain and Sorribes (1987) studied the morphology and palynology of the Cuban *Kalmia* and supported Ebinger's treatment (Table 4).

F. Biosystematic Investigations of *Kalmia*

All *Kalmia* species so far studied have the basic chromosome number of x=12. The chromosome numbers for the Cuban taxa are not known. Except for *K. polifolia* which is tetraploid with 2n=48, all five other North American species are diploid with 2n=24 (Hagerup 1928; Jaynes 1969; Löve 1982a, 1982b). The x=12 is reported to be the ancestral number for the *Ericaceae* which probably had tetraploid origin from the *Epacridaceae* with x=6 (Raven 1975). Attempts to double the chromosome numbers of *K. latifolia* and *K. hirsuta* have not been successful (Jaynes 1988a).

Jaynes started his *Kalmia* crosses in 1961, and so far about 1400 controlled crosses have been made. Although not all of them have been successful, he gained a wealth of information on the breeding behaviour, and genetic control of many characters. At least 40 traits of *K. latifolia* have been identified and inheritance data are available for about 12 of them (see Jaynes' Tables 14-1 and 14-2, 1988a). Many

Table 4. Comparison of Treatments of Cuban *Kalmia* by Various Botanists (PDR=Piñar del Rio; IOP=Isle of Pines)

Botanist(s)	"*ericoides*" variant	"*simulata*" variant	"*aggregata*" variant
Small(1914)	*K. ericoides* PDR	---------	*K. aggregata* IOP
Roig & Acuña (1957)	*K. ericoides* PDR IOP	*K. simulata* IOP	*K. aggregata* IOP
Wood(1961)	*K. ericoides*	*K. ericoides*	*K. ericoides*
Southall & Hardin(1974)	*K. ericoides* PDR IOP	*K. simulata* IOP	*K. aggregata* IOP
Ebinger(1974)	*K. ericoides* var.*ericoides* PDR	*K. ericoides* var.*ericoides* IOP	*K. ericoides* var. *aggregata* IOP
Judd(1983)	"	*K. ericoides* var. *aggregata* IOP	*K. ericoides* var. *aggregata* IOP
Berazain & Sorribes(1987)	"	*K. ericoides* var. *ericoides* IOP	*K. ericoides* var. *aggregata* IOP
Present study	"	*K. ericoides* var. *aggregata* IOP	*K. ericoides* var. *aggregata* IOP

Note: ---: Not treated.

of the traits studied are single gene traits (Jaynes 1970, 1971a, 1971d, 1973, 1974, 1975, 1978, 1981, 1988a), such as the willow-leaved form, *angustana* (a recessive gene *w*), corolla-lacking form, *apetala* (a recessive gene *p*), three polypetalous or nearly polypetalous forms (all under single recessive gene control) which have attracted much attention (Gray 1870; Nicholson 1896; Sargent 1890; Stone 1909; Dudley 1967; Jaynes 1988a). In *K. angustifolia*, the character, white flower versus the red, is also controlled by a single gene, the homozygous recessive (aa) giving white flowers (Jaynes 1971c, 1988a).

In an attempt to improve the mountain laurel's desirable horticultural characters, Jaynes made crosses in all possible taxa combinations, including reciprocals for all *Kalmia* species (except *K. ericoides*). The results (Jaynes 1968a) are shown in Figure 2. The barriers to gene flow are well established and there has been no report of natural hybridization between the species, where the stylar inhibition of pollen tube growth is believed to be the major factor obstructing hybridizing and accounting for the lack of seed set. On the other hand interpopulational crosses within species were successful. No geographic variation was found. Based on his crosses, Jaynes (1968a, 1988a) suggested that *K. angustifolia* and *K. carolina* should be considered as a single species. *Kalmia polifolia* and *K. microphylla* should be recognized as distinct species based on their chromosome numbers (Jaynes 1969). Although they cross readily (Fig. 2), the triploid hybrids are sterile (Jaynes 1988a). Inbreeding depression and selfincompatibility have been observed in *Kalmia* species (Jaynes 1968b). He also tried to cross *Kalmia* species with *Rhododendron* species and *Kalmiopsis leachiana* without success. He consequently expressed doubt about the reports that there exist hybrids between *Kalmia latifolia*

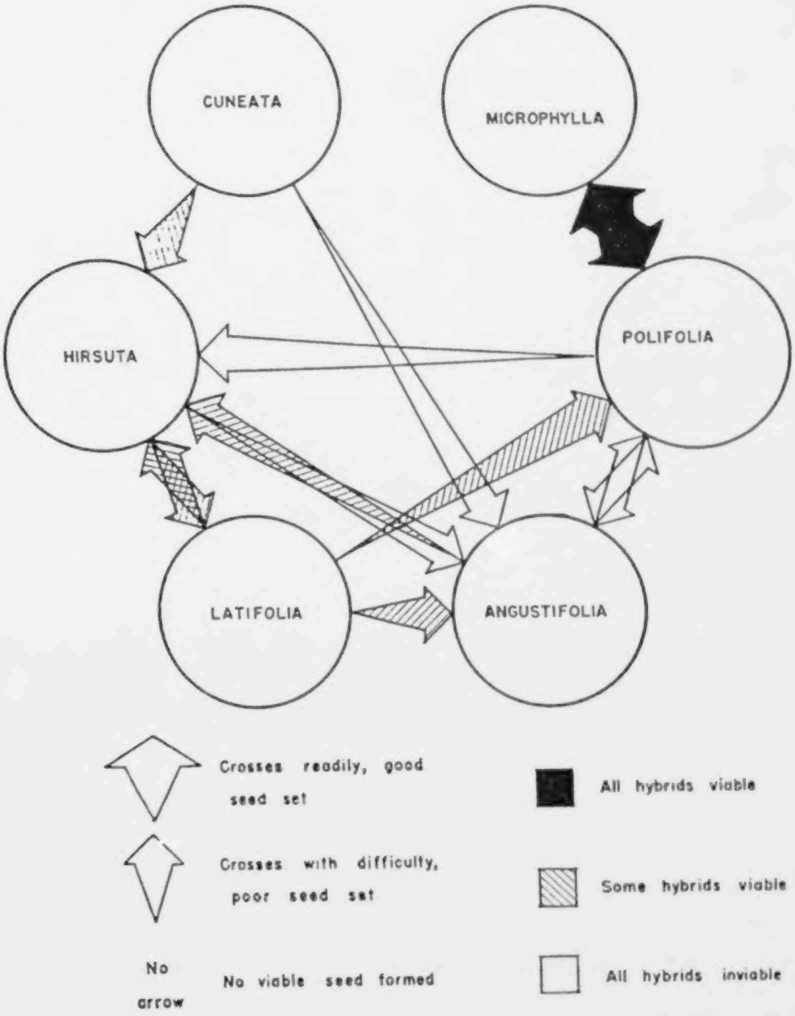
CUNEATA
MICROPHYLLA
HIRSUTA
POLIFOLIA
LATIFOLIA
ANGUSTIFOLIA
Crosses readily, good seed set
Crosses with difficulty, poor seed set
No arrow
No viable seed formed
All hybrids viable
Some hybrids viable
All hybrids inviable

Figure 2. Crossing abilities of 6 *Kalmia* species in all possible F_1 combinations (Jaynes 1968a).

and two rhododendrons, *Rhododendron maximum*, and *R. williamsianum* (Jaynes 1988a). A recent attempt to cross *Rhododendron kawakamii* (♀) with *Kalmia latifolia* (♂) also failed to produce any viable seeds (Kaul *et al.* 1986).

There has been much research on the structural aspects of *Kalmia*. Copeland (1943) studied the floral receptacle, ovule, seed, leaf anatomy of *K. latifolia* and *K. microphylla*. Other features studied have been wood anatomy (Cox 1948), pollen grains of *K. latifolia* (Ikuse 1954), embryology (Ganapathy and Palser 1964), stomatal and pith structure (Watson 1965), leaf structure (Böcher 1981), and pollen grains of *K. polifolia* and *K. angustifolia* (Warner and Chinnappa 1986). In his Ph.D. project, the late R.M. Southall (1973) studied many characters in *Kalmia*, such as their habitat, the comparative morphology of twigs, leaves (size, venation, stomata), inflorescences, flowers, pollen, seeds; phenology, and behaviours in transplant experiments. Ebinger (1974) conducted extensive studies of *Kalmia* morphology based on herbarium specimens, examining over 8,000 specimens of all *Kalmia* species.

Ecological and breeding biology of *Kalmia* have also been evaluated. The mechanism of pollen-discharge is a distinctive feature of the genus, known since at least 1772 (Kress 1988). Ebinger (1974) has reviewed this subject. Recent studies of pollination mechanism and ecology of *Kalmia* involve *K. angustifolia* and *K. polifolia* (Small 1976), *K. microphylla* (Douglas 1983), and *K. latifolia* (Kress 1988; Rathcke 1988a; Real and Rathcke 1988, 1991; Rathcke and Real 1993). Natural soil conditions for *K. polifolia* and *K. angustifolia* were found to be subacid to mediacid peat (Wherry 1920; also see Lynn and Karlin 1985; Karlin and Lynn 1988). *Kalmia polifolia* was one of Reader's subjects in his extensive ecological studies. Plants were collected along a 800 km latitude range in Ontario and transplanted to the University of Guelph Arboretum, Guelph, Ontario, where several environmental effects on the plants were investigated (Reader 1979a, 1979b, 1980, 1982a, 1982b, 1983a, 1983b). Foster and his associates have been very active in unravelling the mechanism of bog development and landform dynamics, and the ecological niche of *K. polifolia* was investigated in their study (Foster *et al.* 1988). Several ecological studies of mountain laurel (*K. latifolia*) have occurred (Kurmes 1961, 1967; O'keefe 1981; Wilson and O'Keefe 1983; Czekalski 1985; Monk *et al.* 1985; Zika and Dann 1985; Cooper and McGraw 1988; Anderson and Egler 1988; Lipscomb and Nilsen 1990a, 1990b; Kittredge and Ashton 1990; Muller 1991). It is also interesting to note that *K. angustifolia* can form a distinctive community type in the subalpine environment (Doyle *et al.* 1987). *Kalmia polifolia* along with black spruce can form another vegetation type (Kurmis *et al.* 1986). The association of fungi with ericaceous plants is of considerable ecological importance and *Kalmia* has been included in such studies (Largent *et al.* 1980; Parmelee and Ginns 1986).

In recent years, it has been difficult to keep up with the introduction of new techniques available to systematists. I believe in the motto "A good cat is the one that catches the rat whether it is black or white" (my translation from Chinese). Botanists have expressed the same idea, for example, Arthur Cronquist (1980) stated that, "Chemical characters are like other characters: they work when they work, and they don't work when they don't work". I think his words also apply to today's situation. In this project, I have used a chemotaxonomic approach, specifically flavonoid survey, using a variety of isolation and identification techniques.

Flavonoids were first used as systematic markers in higher plants in the late 1940's when a Swedish scientist Holger Erdtman and his colleagues applied the technique to *Pinus* species (Swain 1981). Bate-Smith, Alston, Reznik, Geissman, Harborne, and Swain were pioneers in this field (Swain 1981). According to Stuessy (1990), the most influential work on chemical systematics was carried out by R.E. Alston in collaboration with B.L. Turner (both of the University of Texas at Austin) when they applied flavonoid methods to the genus *Baptisia* (*Fabaceae*) in the late 1950's (Alston and Turner 1959; Turner and Alston 1959). Their book "Biochemical systematics" (1963) might rightly be called, as Harborne and Turner (1984) put it, "the first textbook on chemical systematics in the broad sense". There is a tremendous amount of literature in this area. For general discussion one can refer to Alston and Turner (1963), Bisby *et al.* (1980), Crawford (1990), Crawford and Giannasi (1982), Giannasi and Crawford (1986), Grant (1984), Harborne and Turner (1984), Stace (1989), Stuessy (1990), Swain (1963), and Thorne (1992, also for the most recent updated literature in angiosperm classification). General discussions of flavonoids in systematics can be found in a number of publications, such as Bohm (1987), Crawford (1978), Denford (1984), Giannasi (1978, 1988), Gornall and Bohm (1978), Harborne (1967, 1972, 1977, 1980a), Stuessy and Crawford (1983). The progress in flavonoid research has been updated in "The Flavonoids" (Harborne *et al.* 1975, Harborne and Mabry 1980, Harborne 1988). Stafford (1990) reviewed flavonoid metabolism. Rao (1990) reviewed root flavonoids. If one is interested to know about the primary researchers in phytochemistry in the past and present, one should read Harborne's paper entitled "The First Thirty Years - Phytochemists Past and Present" (1991).

Flavonoid techniques have been widely used in the systematics of *Ericaceae*, at the family level (Harborne 1968; Harborne and Williams 1973; Tămaş 1973), subfamily level in the *Monotropoideae* (Bohm and Averett 1989), tribe level in the *Cladothamneae* (Bohm *et al.* 1978), and generic level in *Arctostaphylos* (Denford 1973, 1981; Packer and Denford 1974), *Cassiope* (Denford and Karas 1975), *Cavendishia* (Luteyn *et al.* 1980), *Menziesia* (Bohm *et al.* 1984), *Phyllodoce* (Watson 1977), *Pyrola* (Haber 1983, 1987, 1988; Haber and Takahashi 1988), and *Rhododendron* (King 1977, 1980; Harborne 1980b; Harborne and Williams 1971; Kunishige and Kobayashi 1980; Mabry *et al.* 1975; Spethmann 1974, 1975, 1979, 1980, 1987).

Kalmia species have been used on several occasions in phytochemical studies and Harborne and Williams (1973) first scanned the flavonoid aglycones from *K. latifolia* and *K. angustifolia* in their chemosystematic study at the family level in 1973. A summary of all 24 flavonoids isolated and identified previously from *Kalmia* is shown in Table 5. The present project is the first attempt to utilize flavonoid techniques in *Kalmia* systematics. Because of the diversity of flavonoid profiles in *Kalmia* species, the chemosystematics of *Kalmia* could be pursued, in an attempt to clarify and understand the systematic relationships and phylogeny of the group.

Table 5. Flavonoids from *Kalmia* Reported in the Literature

Flavonoid	Source	Reference
Flavone		
1. Eucalyptin	lat	Wollenweber and Kohorst (1981)
2. 8-desmethyl-eucalyptin	lat ang pol	"
3. Sideroxylin	lat	"
4. 8-desmethyl-sideroxylin	lat ang pol	"
Flavonol		
5. kalmiatin	lat	Wollenweber and Kohorst (1984)
6. 8-desmethyl-kalmiatin	lat	"
7. latifolin	lat	"
8. 8-desmethyl-latifolin	lat	"
9. quercetin	lat ang	Harborne and Williams (1973)
	lat	El-Naggar and El-Feraly et al. (1980)
9.1 hyperin	lat	Sakakibara et al. (1976)
	lat	El-Naggar and El-Feraly et al. (1980)
9.2 guaijaverin	lat	"
10. gossypetin	lat ang	Harborne and Williams (1973)
10.1 3-O-galactoside	lat ang	Harborne and Williams (1969)
Catechin		
11. (+)-catechin	lat	El-Naggar and El-Feraly et al. (1980)
Dihydrochalcone		
12.phloretin	lat	"
12.1 phloridzin	lat	Bridel and Kramer (1931)
	lat	Williams (1964)
	lat	Sakakibara et al. (1976)
	lat	Mancini and Edwards (1979)
	lat	El-Naggar and El-Feraly et al. (1980)
12.2 phloridzin 2"acetate	lat	"
13. 3-hydroxyphloretin	lat	"
13.1 3-hydroxyphloridzin	lat	"
13.2 3-hydroxyphloridzin 2"-acetate	lat	"
14.1 4-O-methylphloridzin	lat	"
15.1 Asebotin	lat	Bourquelot and Fichtenholz (1912)
	ang	Williams (1964)
	lat	Mancini and Edwards(1979)
Flavanone		
16. eriodictyol	lat	El-Naggar and El-Feraly et al. (1980)
Anthocyanins		
17.1 cyanidin-3-O-(?)glucoside	ang	Santamour and Lucente (1967)

Note: lat = K. latifolia; ang = K. angustifolia; pol = K. polifolia.

II. Materials and Methods

A. Materials used in this study

Kalmia materials for this study were collected in the summers of 1989, 1990 and 1991 throughout its range in North America. Fresh material of the Cuban species, *K. ericoides*, could not be obtained for study, herbarium specimens were used in the population scan. A voucher specimen for each population collected was deposited at the University of Alberta Vascular Plant Herbarium (ALTA). Each collection includes dried leaves, live plants, and specimens of the associated species. Some collections also include preserved floral buds and seeds depending on the season of collection. A list of all *Kalmia* collections is in Part I of Appendix 1 (Figs. 14-18).

In this study, the isolation of flavonoids was carried out several times. Most flavonoids were isolated in the first isolation which used the material (ca. 1 kg of dried leaves) pooled from populations of all *Kalmia* species except *K. ericoides*. As far as there was enough material, leaves (about five grams) were taken from each population and put together for the isolation. The following collections were used for this purpose (collection number is given here, refer to Appendix 1 for more information): *Kalmia angustifolia* var. *angustifolia* 9107, 9109, 9112, 9113, 9115, 9116, 9119, 9120, 9123-27, 9129, 9131-33, 9135, 9143-45, 9148, 9149, 9151; *K. angustifolia* var. *carolina* 9160-64, 9177, 9180, 9181; *K. cuneata* 9165; *K. hirsuta* 9182-96, 9198-91107; *K. latifolia* 9136-42, 9146, 9147, 9150, 9152-59, 9166-76, 9178, 9179, 9197. *K. microphylla* AB-001, AB-005, AB-006, BC-003-009, YT-001, YT-002, 9001, 9043-48, 9050-55, 9058-67, 9070, 9071; *K. polifolia* AB-001, AB-002, AB-004, 9004, 9005, 9008, 9010, 9011, 9013-16, 9018, 9019, 9026, 9033, 9037, 9040-42, 9101-9106, 9108, 9110, 9111, 9114, 9117, 9118, 9121, 9122, 9128, 9130, 9134.

The second round isolation was carried out after the preliminary flavonoid scan at the population level because some populations of certain species exhibited flavonoids not obtained in the first isolation. This time the isolation targeted specific flavonoids in specific populations. Each species was treated individually, that is, the materials from each species were amalgamated (ca. 250 grams) and isolated for flavonoids separately. The materials used were: *Kalmia angustifolia* var. *carolina* 9162, 9163, 9164; *K. hirsuta* 91100; *K. latifolia* 9152, 9178, 9179; *K. polifolia* 9006, 9018, 9027, 9033, 9041, 9042, 9101, 9103.

The survey of flavonoids in *Kalmia* was carried out in the population scan. In the scan, 1-3 g of dried, ground leaves from each collection was soaked in 80% methanol for at least a week before the extract was concentrated and applied to paper chromatographic analysis. Besides the populations collected by the author (Appendix 1, Part I), some populations (or individuals) were surveyed from herbarium specimens and only one to a few leaves was taken and soaked in the 80% methanol. In Appendix 1, Part II, most of the populations listed belong to this category (Figs. 14-18). Other collections listed in Part II were obtained from several institutions in North America (denoted by a "*" at each entry) (Figs. 14-18). For each collection, date of the specimen chosen was as close as possible to those of the most of the populations scanned. This was to reduce the effect of seasonal flavonoid fluctuations. Materials used for population scan were all leaves, young and old, though young twigs may be present in *Kalmia polifolia*, *K. microphylla*, and *K. hirsuta* due to their size. This was done because, as in some other plants (Giannasi 1978; Stuessy and

Crawford 1983), different organs tend to produce different flavonoids in *Kalmia* (unpubl. data).

In the Summer of 1992, at the *Kalmia polifolia* collection site AB-004 (Fort McMurray, Alberta, Canada), six plants were chosen to compare the flavonoid profiles of air dried leaves and fresh leaves. The fresh leaves were soaked in 80% methanol on site and the rest of the leaves from the same plant were air dried first and extracted with 80% methanol. Both sets of materials stayed in 80% methanol for a week before analysis.

B. Flavonoid Chemistry

The isolation and identification of *Kalmia* flavonoids was carried out using standard procedures (Harborne *et al.* 1975; Mabry *et al.* 1970; Markham 1982; Harborne 1989). The basic techniques used in this laboratory were described by Downie and Denford (1986).

In this study, all extractions were carried out using 80% methanol to soak the ground leaves while being stirred in blender. The extraction was repeated for three to five times. The resultant solutions were vacuum evaporated to dryness. The residues were partitioned following the procedure described by El-Naggar and Doskotch *et al.* (1980). Each partitioning fraction (water, n-butanol, ethyl acetate, hexane, chloroform) was checked for flavonoids using Thin-layer Chromatography (TLC) or paper chromatography (PC). Three fractions were found to contain flavonoids: ethyl acetate, n-butanol, and chloroform. The ethyl acetate and n-butanol fractions were found to contain basically the same flavonoids and were combined. The separation of flavonoids in chloroform or the combined fractions were carried out using all available chromatography techniques: 1) column, including Polyclar AT, silica gel G., and Sephadex LH-20; 2) paper, Whatman 3mm and 1mm; and 3) TLC, cellulose and silica gel G. The isolation of a flavonoid may involve one to all the chromatography methods mentioned above. All the flavonoids isolated were further purified by TLC or paper chromatography, followed by column isolation using Sephadex LH-20. Once purified, the identification of each flavonoid followed Downie and Denford (1986). For comparison, standard flavonoids were obtained from Sigma, U.S.A., Fisher, Canada, and Extrasynthese (21 Lyon-Nord, B.P. 62, 69731, Genay, France) and as gifts from such researchers in the field as Drs. Doskotch (Pharmacy, Ohio State University) and Wollenweber (Institut für Botanik der Technischen Hochschule, Darmstadt, Germany). The known flavonoid profiles of *Kalmia* related genera, such as *Andromeda*, *Ledum*, *Rhododendron*, *Phyllodoce*, *Menziesia*, and *Elliottia* were also scanned using 2-dimensional (2D) paper chromatography (PC) for comparison.

In the population scan, solvents used for developing the 2D PCs were BAW, n-butanol(6) : acetic acid(1) : water(2), and AW, acetic acid(15%) : water(85%). Whatman 3mm chromatographic paper (Fisher, Canada), was used in this study. The PCs were viewed and scored for flavonoids under the UV light (360 nm) with addition of ammonia fumes (50% in water).

C. Numerical Analyses

The tabular form of flavonoid profile presentation without any kind of multivariate statistical analysis has been a quite common practice since the beginning of the flavonoid systematics, even though multivariate statistical analysis has become routine in systematics during the same period of time (Wolf and Whitkus 1987). In recent years, some workers have integrated flavonoid profiles with other characters in their multivariate or cladistic analyses (Wolf 1981; Downie 1987; Gruezo 1988), but only a few systematists have used flavonoids as sole characters in their statistical analysis (Bohm *et al.* 1984; Wolf and Whitkus 1987).

In the present study, a total of 248 populations (OTU's) from all *Kalmia* species were scored for the 76 flavonoids isolated. The score for each flavonoid (a spot on the 2D PC) is based on an optical four-scale-method, that is 0 = not detectable, 1 = detectable, 3 = highly concentrated, 2 = concentration falling between 1 and 3. The relative concentration of flavonoid spots on the same paper chromatogram was used in the concentration assignment. The argument against using a binary, present or absent method as Bohm *et al.* (1984) or Wolf and Whitkus (1987) did, is as follows: 1) not detectable does not mean the flavonoid is absent (Crawford 1978; Stuessy and Crawford 1983), i.e. not detectable and barely detectable are not so different as to deserve the qualitative treatment; 2) much information would be lost if one gave the hardly detectable and the highly concentrated flavonoid equal weight; 3) even though it can be somewhat subjective in distinguishing the intermediate, scale 2, from scales 1 & 3, the information gained should outweigh subjectivity. On the other hand, with purely present and absent scaling one still encounters the problem of achieving objectivity (but for comparison, the binary method was also tested in this study, see footnote 2, p. 79).

Variation in flavonoid profiles was first examined using cluster analysis of OTU's to detect whether populations of the taxa formed cohesive groups. The reason that cluster analysis, a phenetic analysis, was used instead of a cladistic analysis is that of the difficulty encountered in polarity determination. The outgroup of *Kalmia* is not clear from the available flavonoid data. Although the present study indicates the outgroup should be sought in *Rhododendron* or its close relatives, it would be very difficult to determine which species or group of species of *Rhododendron* should serve as the outgroup of *Kalmia*. This is because *Rhododendron* is a rather formidable taxonomic group with ca. 1200 species described (Heywood 1978). It would be unwise to use the proposed evolutionary scheme for flavonoids to designate polarity because reductions in flavonoid structure are common (Gornall and Bohm 1978). In this study, phenograms were produced, based on taxonomic distances (computed by program NTSYS), with unweighted pair-group method using averages (UPGMA), which is widely used in ecology and systematics (James and McCulloch 1990; M.R.T. Dale 1992, personal communication).

Ordination techniques were used to corroborate the cluster analysis. Both principal component analysis (PCA) and principal coordinate analysis (PCO) were run on all data sets. Since PCO showed basically the same result in every analysis as PCA did, only the results of PCA are presented and discussed in this study. PCA is chosen because it is by far the most widely used multivariate type of ordination in ecology and systematics (James and McCulloch 1990). The product-moment correlation was adopted in the PCA as recommended by R.J. Bayer (1992, personal communication).

All the analyses were performed with the NTSYS-pc program package (Version 1.2, Rohlf 1987), supplied by Dr. R.J. Bayer. Both cluster and PCA analyses were performed directly using the population or specific flavonoid distribution data without any standardization since only one kind of scaling is involved. The resultant phenograms were redrawn by hand and the PCA data were imported into SigmaPlot program

(Version 5.0, developed by Jandel Corporation, 1986-1992), owned by the Department of Botany, to generate laser printout on an HP laser printer. All analyses were performed on IBM personal computers or compatibles.

The overall flavonoid distributions among all the species were determined and six sets of analyses were carried out to explore different questions of relationships within the genus. 1) all populations of the *Kalmia angustifolia - carolina* complex (45 OTU's) were analyzed to determine whether they form two discrete groups. 2) *Kalmia ericoides* and *K. hirsuta* (34 OTU's) were grouped together to test the proposed descendant - ancestor relationship between the two species (Southall and Hardin 1974), and to determine whether populations of *K. ericoides* diverge into two distinct groups. 3) the relationship between *Kalmia polifolia* and *K. microphylla* (124 OTU's) was explored. 4) all populations from *K. microphylla* (66 OTU's) were analyzed together to determine if there are further separations within the species and if there exist any patterns in the geographical distribution of the flavonoids. 5) all populations were analyzed simultaneously (248 OTU's) to identify the overall patterns of similarities within the genus. 6) aglycone profiles from all seven species were analyzed to determine if it is possible to separate them based solely on aglycone profiles. The basic data matrices are presented in Appendices 2 and 3.

III. Results

A. Flavonoid Chemistry

A total of 76 flavonoids was isolated and 53 of them were identified or partially identified with the remaining 23 being tentatively assigned to established structures. A complete list of flavonoids isolated is presented in Table 6, and chromatographic and spectral data for these compounds are presented in Table 7. A composite two-dimensional chromatogram of all flavonoids is illustrated in Figure 3, and the ordered listing of flavonoids in the Figure can be found in Appendix 4. The flavonoid distributions of seven *Kalmia* species were generated after the population scan. Three sets of data are presented: 1) all population flavonoid profiles, 248 in total, are presented for each species in Appendix 2; 2) Table 8 and Part I of Appendix 3 provide information about the flavonoid distributions for 7 species; 3) the aglycone distributions of the 7 species can be found in Table 9 and Part II of Appendix 3. The aglycone distribution presents the number (or percentage) of populations in a species that can produce a certain aglycone either in the form of a free aglycone or a glycoside. Both Table 8 and Table 9 give symbolic illustrations of flavonoid distributions, the actual population numbers and percentages calculated from Appendix 2 for each species are presented in Appendix 3.

Some flavonoids tend to crowd together on PC or overlap, different situations were treated differently. Since the flavonoids 8-desmethyl eucalyptin and 8-desmethyl sideroxylin have almost the same Rf values and they overlap completely, they were treated as one flavonoid in the

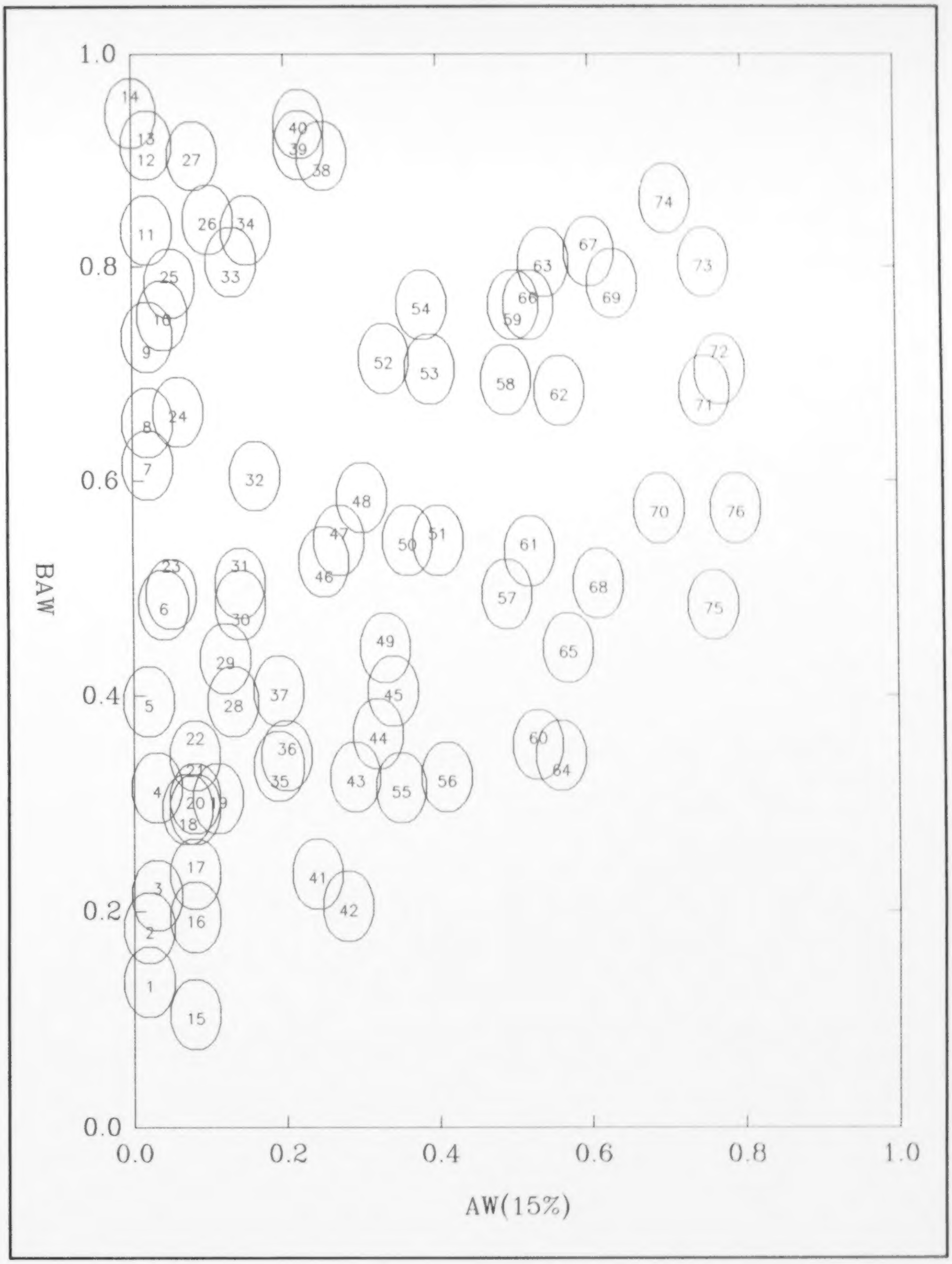

Figure 3. A composite 2-dimensional chromatogram of *Kalmia* flavonoids (see Table 6 & Appendix 4 for identity).

Table 6. A List of Flavonoids Isolated From *Kalmia*

Flavone	
1. 8-desmethyl eucalyptin (mixed with 13)	12*
2. 8-desmethyl sideroxylin	13
2.1 -5-O-arabinoside	31
3. Undetermined	71
Flavonol	
4. 8-desmethyl kalmiatin	27
5. Kaempferol	11
5.1 3-O-rhamnoside	59
5.2 3-O-arabinoside	54
5.3 3-O-rutinoside	65
6. Quercetin	8
6.1 3-O-galactoside (hyperin)	50
6.2 3-O-galactoside derivative	44
6.3 3-O-galactoside derivative	49
6.4 3-O-glucoside	36
6.5 3-O-arabinofuranoside (avicularin)	47
6.6 3-O-arabinopyranoside (guaijaverin)	52
6.7 3-O-rutinoside	60
6.8 3-O-galactosylglucoside**	56
6.9 3-O-rhamnosylarabinoside**	58
6.10 7-O-glucoside	16
6.11 3'-O-glucosylgalactoside**	18
6.12 3'-O-glucosylxyloside**	23
7. Quercetin-3-O-methyl ether	26
7.1 3'-O-xyloside	32
8. Isorhamnetin	9
8.1 3-O-galactoside	53
8.2 3-O-arabinoside	48
9. Quercetin-3,5,3'-tri-O-methyl ether ? (new?)	67
10. Gossypetin	4

Table 6 Continued

10.1 3-O-galactoside	55
10.2 3-O-monoglycoside	42
11. Myricetin	5
11.1 3-O-galactoside	43
11.2 3-O-glucoside	41
11.3 3-O-rhamnoside	51
11.4 3-O-arabinopyranoside	46
11.5 3-O-arabinofuranoside	35
11.6 3'-O-glucoside	1
11.7 3'-O-xyloside	3
11.8 5'-O-xyloside(?)	2
12. Myricetin-3-O-methyl ether	24
12.1 3'-O-xyloside	22
12.2 3'-O-glucosylxyloside**	19
Undetermined glycosides	
Ufg.1 ?-glycoside	64
Ufg.2 7-glycoside	15
Ufg.3 7-glycoside	29
Chalcone	
13. Aglycone#1	25
14. Aglycone#2	33
15. Aglycone#3	38
Glycosides:	
Cg.1 glucoside	45
Cg.2 glycoside	17
Cg.3 glycoside	37
Aurone	
16. Aglycone #1	7
16.1 ?-O-rhamnoside(?)	28
16.2 ?-O-glucoside	21

Table 6 Concluded

17. Aglycone#2	10
17.1 glycoside(1)	6
17.2 glycoside(2)	20
17.3 glycoside(3)	30
Dihydroflavonol	
18. Taxifolin (dihydroquercetin)	66
18.1 3-O-glucoside	75
18.2 3-O-xyloside	70
Catechin	
19. D(+)-catechin	61
Dihydrochalcone	
20. Phloretin (2',4',6',4,-tetramethoxy dihydrochalcone)	39
20.1 2'-O-glucoside (phloridzin)	62
20.2 2'-O-glucoside monoacetate	73
21. 3-hydroxy phloretin	34
21.1 2'-O-glucoside (3-hydroxy phloridzin)	57
22. Asebogenin (phloretin-4'-O-methyl ether)	40
22.1 2'-O-glucoside (asebotin)	69
22.2 2'((?)-O-galactosylxyloside**(new?)	76
23. Asebogenin-C-methyl ether (?) (new?)	14
Flavanone	
24. #1 (glycoside)	72
25. #2 (aglycone not isolated)	
25.1 glycoside(1)	63
25.2 glycoside(2)	68
26. #3 aglycone	74

Notes: *: number corresponds to the spot number on 2-D paper chromatogram chart (Figure 3).

**: the order of the sugar attachment is not established.

Table 7. Some of the Properties of *Kalmia* Flavonoids

	Colour[1]		Rfs		Absorption maxima[2] in nm					
Flavonoid	UV	$+NH_3$	BAW	AW	MeOH	NaOMe	$AlCl_3$	+HCl	NaOAc	$+H_3BO_3$
Flavone										
1	P	P	.91	.02	276	274	248s	262s	274	276
					330	298s	262s	288	330	294s
						334	288s	302	388	332
						388	304	348		
							254	384s		
2	P	P	.91	.02	278	276	288	288	276	278
					328	328	302	300	330	330
							352	348		
2.1	P	1P	.50	.14	274	232s	276	286	274	276
					330	270	298s	300	334	334
						388	352	348	386	
							388s	388s		
3	B	YG	.68	.75	246	266	268	246	270	264
					300s	310	310	272s	300	304
					330	374	358	300s	350	340
								328		
Flavonol										
4	P	P	.90	.08	276	276	276	284	272	276
					332	296	308	302s	328	328
						332	342s	352		
							410s	390s		
5	Y	Y	.83	.02	266	276	242	242	276	270
					296	320	256s	256s	310	320
					322	404d	260s	260s	392	370
					364		266	266		
							272	272		
							306	306		
							350	350		
							424	424		
5.1	P	YG	.76	.50	266	276	276	276	276	268
					286	330	302	302	330	288
					342	390	346	342	378	344
							398	392		

Table 7 Continued

5.2	P	YG	.76	.38	268 284s 350	276 324 398	274 302s 350 398	252s 278 304 348 398	276 306 382	268 298s 356
5.3	P	YG	.44	.57	266 302 352	266s 274 326 402	272 304 350 390s	276 302s 348 392	272 304s 390	268 332 354
6	Y	Y	.65	.02	256 270s 302 372	248 276 332 408d	256s 272 302s 444	266 272s 302 360 430	276 332 398d	260 296 390
6.1	P	YG	.54	.36	258 360	266s 274 332 406	268 274 298 420	268 274s 302 360 402	266s 274 330 394	264 300s 378
6.2	P	YG	.36	.32	256 268 290 360	268s 276 322 408	278 302s 436	276 300 366 400	276 316 388	264 298 380
6.3	P	YG	.44	.33	262 290s 360	274 324 408	274 302s 430	268 298s 366 404	276 326 392	250s 264 302 380
6.4	P	YG	.34	.20	258 264 292 360	264 276 322 406	278 302s 434	276 300s 362 398	260 274 302 384	258 298 380
6.5	P	YG	.54	.27	254 266s 298 358	266 274 326 406	274 302 436	266 272s 302 360 410	266s 274 324 390	262 302 378
6.6	P	YG	.71	.33	256 266s 300 354	266s 274 330 404	266s 274 302s 426	272 300s 362 402	266s 274 324 386	258s 264 296s 376

Table 7 Continued

6.7	P	YG	.35	.53	256 266 298 358	268s 274 324 410	268 272 302s 420	268 274s 302s 358 398	266 272s 320 392	256s 264 272s 298 376
6.8	P	YG	.32	.41	256 264s 302 358	266 274 330 406	268 272 302s 420	272 298s 366 398	256s 276 326 388	254 306 378
6.9	P	YG	.69	.49	254 264s 302 350	266s 272 328 392	268 276 302s 430	268s 274 296s 356 398	266s 272 324 382	262 368
6.10	lY	lY	.19	.08	260 370	262 418d	266 272s 432	266 272s 358 426	264 392	262 294s 386
6.11	lY	lY	.29	.07	266 366	266 272s 302s 324s 396	264 302s 354 424	262 302s 354 424	272 320 394	264 272 370
6.12	Y	Y	.49	.05	252 266s 324 368	266 276 324 410	262 272s 302 352 424	262 272s 302 352 424	268s 276 322 404	252 268 306 324 372
7	P	YG	.84	.10	254 258 268s 292s 300s 358	266 274 328 406	266s 276 302s 434	266 276s 302 360 400	268s 274 324 394	262 272s 300 378
7.1	P	YG	.60	.16	250 270 352	266 276 328 402	252s 280 306 358 400	252s 282 304 352 398	252s 278 328 400	252s 270 358

Table 7 Continued

8	Y	Y	.73	.02	252 266s 302 368	266 274 324 412d	266 272s 302s 356s 428	264 272s 302s 356 428	270s 276 322 404d	254 262s 272s 304 374
8.1	P	YG	.70	.39	252 264 270s 302 358	272 300 408	256s 264 302 410	266 274s 302 362 404	266s 274 304 388	262 310 380
8.2	P	YG	.58	.30	256 266s 304s 358	258s 286 326 422	262 274 366 406	258 278 364 398	274 322 384	266 294s 378
9	B	lB	.81	.60	254 260 298 344	240 278 390	256 262 298 344	256 262 298 344	278 390	254 260 298 346 390s
10	P	P	.31	.03	262 278 310 340 384	246s 282 380	256 280 380 454	272 314s 374 446	276 374	250s 266s 294s 358
10.1	dP	PY	.31	.35	282 376	292 438	276 396	278 376	286s 434	286 396 434s
10.2	P	PY	.20	.28	274 364	274 418	284 440	280 420	not done	
11	Y	Y	.39	.02	254 264s 302 330s 374	258s 264s 286 320d	266 272 302s 452	262 274 310 358 432	258s 262s 334d	252 258s 272s 304 392

Table 7 Continued

11.1	P	YO	.32	.29	256 266s 308 366	260 274s 322 406	266 274 304s 432	266 276 310 370s 408	256s 276 328 388	258 304 384
11.2	P	YO	.23	.24	268 302s 358	272 318s 404	280 436	274 356s 398	274 310s 390	286 378
11.3	P	YO	.54	.40	254s 266 288 352	270s 290s 326 392	276 312s 422	276 308 360 398	274 328 386	292 372
11.4	P	YO	.52	.25	266 272 360	276 394	278 308s 428	278 306 364 404	276 302 386	276s 284 370
11.5	P	YO	.33	.19	254s 266 300 362	272 322 404	276 312s 432	276 306s 366s 408	254 276 324 386	256s 266 302s 382
11.6	Y	Y	.13	.02	252 268 298 370	246 332d	258 276 440	274 308s 428	252s 278 334 404d	300 364 388
11.7	Y	Y	.21	.03	252 266s 302 370	248s 282 334 414d	264 272 310s 352s 442	264 272s 310 354 430	250 278 334 410d	298 334 390
11.8	Y	Y	.18	.02	250 300 372	276 332 440d	276 364 440	276 364 428	254s 274 334 402	254s 300 388
12	P	YO	.66	.06	252 264s 272s 304s 362	260 272s 330s 406	274 310s 440	276 308 372 404	256s 266 276 326s 392	256s 268 272s 304s 382

Table 7 Continued

12.1	P	Y	.34	.08	252 270 302s 358	274 330 412	258 276 310s 368s 424	278 302s 358 398	266 274s 322 404	262 378
12.2	P	Y	.30	.11	252 270 354	268 274 332s 408	266 366s 432	268 302s 354 398	250s 278 324s 406	254 302s 376
Ufg.1	CO	CO	.34	.56	254 296 356	256 278s 312 330 394	266 272s 306 376 440s	264 362 410s	260 272s 350 388s	258 298 352s 360 388s
Ufg.2	lY	lY	.10	.08	258 272s 304 374	280 334 410d	276 302s 444	274 302s 364 432	280 330 398d	264 302s 390
Ufg.3	lY	Y	.43	.12	not isolated					
Chalcone										
13	Pi	Pi	.78	.05	272s 291 334 351 363s	275 288s 393	306 318s 368 395	297 355	277 286 396	271s 291 331 353 362
14	Pi	Pi	.80	.13	266s 291 332 351s 365s	275 288s 393	303 375 391	280s 299 356	275 290s 396	275 329 355
15	Pi	Pi	.90	.25	272s 291 333 350 362s	279s 287 395	305 377s 393	297 355	278 286 397	268s 286 329 348s 366s

Table 7 Continued

Cg.1	BP	GB	.40	.34	256 288 336s 358	262 272s 330 408	262s 290 318s 396	268 316 366	262 332 408	256s 292 364
Cg.2	BP	GB	.23	.08	254s 292 338s 360 370s	262s 290 330 406	258 264s 280s 378s 392	262 316s 366 376s	332 406	290 360
Cg.3	BP	GB	.40	.19	254 292 338s 358 370s	246 334 408	250 298 320 384s 396	250 292s 324 374	260 334 408	256s 294 364
Aurone										
16	YG	O	.61	.02	252 276 328 398	276 332 392 484	278 300s 346 516	276 300s 340 398	272 328s 440	284 330 426
16.1	bY	O	.39	.13	256s 278 326 404	292 310 478	286 328s 440	280 318 404	288 322 412 462s	284 324 432
16.2	Y	O	.30	.08	252 274 334s 402	246 272 370s 456	256 276 326 440	256 276 320 400	252s 280 420	268 338 426
17	YG	Y	.75	.04	256s 332s 390	284 364 450	262s 352 392 454	274 332s 352s 392 440s	274s 330 402	256s 330 394
17.1	G	Y	.48	.04	282 320 394	290 364 436	not done			
17.2	G	Y	.29	.08		not done				
17.3	G	Y	.48	.14	288s 394	274s 444	not done			

Table 7 Continued

Dihydroflavonol										
18	P	P	.76	.52	290 324s	244s 326	294s 314 378	278s 312 374	264 326	268 290s
18.1	P	P	.48	.76	292 328s	246 330	294 376s	270s 290s 312 378	248s 292s 332	296 332s
18.2	P	P	.57	.69	294 332s	246s 330	294 372s	272 310 372	272 330	296 324s
Catechin										
19	1P	B	.53	.52	226 282	290 322s	282	282	282	288
Dihydrochalcone										
20	P	P	.91	.22	224 286 322s	242s 322	220 310 366	220 308 366	290s 320	254s 290 320s 340s
20.1	P	P	.68	.56	224 284	244 270 322	264s 292s 308 364s	262 308 364	250s 294s 324	286 330
20.2	P	P	.80	.75	286 324	242 326	310 358s	288s 308 358s	292s 326	288 330s
21	P	O	.83	.15	224 288 322s	242s 322	220s 276s 308 366	220s 276s 308 366	292s 320	258s 292 310s 340s
21.1	P	O	.49	.49	220 286 322s	242s 324	234s 272s 308 358	234s 276s 308 358	250s 294s 324	290 332
22	P	P	.93	.22	286 324s	242 296 362	302 310 374	302 310 374	242s 290 362	286 332s

Table 7 Concluded

22.1	P	lPB	.78	.63	284 316s	282 316s	262s 270s 308 360s	270 306 360s	284 316s	284 316s
22.2	lP	lWB	.57	.79	284 316s	284 316s	286s 306 364s	278s 288s 306 358s	286 316s	286 316s
23	P	P	.94	.00	288 332s	240s 294 364	288 366	290 302 310s 360	292 360	294 310s 344s
Flavanone										
24	lP	GB	.70	.77	300s 312	240s 312 358	300s 312	300s 312	272s 300s 312 352s	300s 312
25										
25.1	lP	B	.80	.54	286 314	272s 290 300s 310s 360	294 312	288 312	288 314 354s	288 314
25.2	lP	B	.50	.61	284 314	288 314s 360	292 312	286 314	282 314 354s	290 316
26	lP	PB	.86	.70	218 284	238 330	224 270 292s	220 276	274 330	274 324s

Notes:

1. Colour changes:
   B = blue; b = bright; C = cream; d = dark in colour, decomposition in spectra-scan; G = green; l = light; O = orange; P = purple; Pi = pink; W = white; Y = yellow.

2. Maxima:
   s = shoulder; d = decomposition.

Table 8. Flavonoid Distributions in *Kalmia*

Flavonoid	*lat*[a] (40)[b]	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2[c]	+++[d]	+++		+++	+++		+++
2.1		+		++	+		
3	+	++	++	+	+++	+++	+++
4	+++						
5			+		+		+
5.1			+++	++	+++	+	+
5.2				+++	+++	+	+
5.3			+++	++			+
6	+++	+++	+++	+++	+++	+++	+++
6.1	+++	+++	+++	+++	+++	+++	+++
6.2				+++		+++	+++
6.3						+++	+++
6.4						+++	
6.5	+	+++	+++	+++		+++	+++
6.6	++	+++	+++	+++	+++	+++	+++
6.7		+++	+++	+	+	++	+++
6.8						+	+
6.9	+++	+++	+++	+++	+++	+++	+++
6.10	+	+++	+++	+++	+++	+++	+++
6.11			+++	+	+	++	++
6.12					+++	+++	+++
7		+					
7.1		++	+++				
8							
8.1						++	+++
8.2							++
9	+++	+++		+	+++	+++	++
10							+
10.1	++	+++		++	+	+++	+++
10.2						+	++
11					+	+++	+++
11.1					++	+++	+++
11.2						+++	+++
11.3					+++	++	+
11.4					+++	+++	
11.5						+++	+++
11.6						+++	+++
11.7						+++	+++
11.8							+++
12						+	++
12.1		+				+	+
12.2						+	++
Ufg.1		+++	++			+++	+++
Ufg.2						++	+++
Ufg.3			++	+++	+	++	+++

Table 8 continued

Flavonoid	*lat*	*ang*	*cun*	*eri*	*hir*	*mic*	*pol*
13		+					
14		+					
15		+					
Cg.1	+++	+++					
Cg.2		+++					
Cg.3	+++	+++					
16	+++	+				+	
16.1	+++	++				+	
16.2	+++						
17			+		+		+++
17.1							++
17.2							+++
17.3	+++	+++	+		+++		+++
18							
18.1						+	++
18.2						+	+++
19	+++	+++	+++	+++	+++	+++	+++
20	+++					+	
20.1	+++					+	
20.2	+++						
21	+++						
21.1	+++						
22	?	+++		++		++	
22.1	+	+++				++	
22.2	+++	+++		+++	+++	++	
23	?	?		?	?	?	
24		+++	+++	+++	+++	+++	+++
25							
25.1		+++					
25.2		+++					
26		+		+++		+	
Total Flavonoids	27	34	19	24	27	47	46

Notes:

a. *Lat* = *K. latifolia*; *ang* = *K. angustifolia*; *cun* = *K. cuneata*; *eri* = *K. ericoides*; *hir* = *K. hirsuta*; *mic* = *K. microphylla*; *pol* = *K. polifolia*.

b. Number in parentheses is the number of populations scanned for flavonoids.

c. Refer to Table 6 for the flavonoid identity.

d. Percentage of populations having the flavonoid:
+ = 1-33%; ++ = 34-66%; +++ = 67-100%;
no entry = absent.

Table 9. Flavonoid Aglycone Distributions in *Kalmia*

Flavonoid	*lat*[a] (40)[b]	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2[c]	+++[d]	+++		+++	+++		+++
3	+	++	++	+	+++	+++	+++
4	+++						
5			+++	+++	+++	+	++
6	+++	+++	+++	+++	+++	+++	+++
7		++	+++				
8						++	+++
9	+++	+++		+	+++	++	++
10	++	++		++	+	+++	+++
11					+++	+++	+++
12		+				+	+++
13	+++	+++					
14	+++	+++					
15	?	?					
16	+++	++				+	
17	+++	+++	++		+++		+++
18						+	+++
19	+++	+++	+++	+++	+++	+++	+++
20	+++					+	
21	+++						
22	+++	+++		+++	+++	++	
23	?	?		?	?	?	
24		+++	+++	+++	+++	+++	+++
25		+++					
26		+		+++		+	
Total Aglycones	16	18	7	11	12	16	13

Notes:

a. *Lat = K. latifolia; ang = K. angustifolia; cun = K. cuneata; eri = K. ericoides; hir = K. hirsuta; mic = K. microphylla; pol = K. polifolia.*

b. Number in parentheses is the number of populations scanned for flavonoids.

c. Refer to Table 6 for the flavonoid identity.

d. Percentage of populations having the flavonoid:
+ = 1-33%; ++ = 34-66%; +++ = 67-100%;
no entry = absent.

Flavonoid 23 (Table 6) cannot be scored on PC because it is, due to its Rfs (BAW 0.94, and AW 0), mixed with the non-polar compounds, e.g. chlorophylls, which are very hard to separate from flavonoid 23. The common practice of using chloroform partitioning against aqueous solutions would still put flavonoid 23 and other non-polar compounds together and it is impractical to resort to column chromatography to determine its presence for all populations. Since there is little doubt that it is a methylated dihydrochalcone (Table 7), a specialized form of phloretin, and by extrapolation, only the species having dihydrochalcone aglycones 20-22 can have flavonoid 23, so all *Kalmia* species except *K. polifolia* and *K. cuneata* could have this flavonoid. The score for this compound is "0" in the population scans, "?" in specific flavonoid distributional tables for five species that could have it. This aglycone was not included in analyses because of the difficulty involved to determine its presence. Some flavonoids slightly overlap and their identities and scores are determined based on not only the Rfs, but also the subtle colour changes, such pairs are 6.2 & 11.1, 6.4 & 11.5, 6.6 & 11.4, and 11.7 & 11.8 (Table 6).

In the experiment of fresh vs. dried leaf flavonoids with collections of *Kalmia polifolia* (site AB-004, Fort McMurray, Alberta), both sets showed the same flavonoid profiles. The flavonoid aglycone zones on PCs from dried leaves are a little more concentrated than their fresh leaf counterparts, indicating there was some degradation during the drying process. Therefore precautions should be taken when handling the leaf samples for flavonoid study, especially when the leaves are leathery and hard to dry. One should dry leaf samples as soon as possible in order to keep degradation to a minimum.

The flavonoid profile of *Kalmia* is extremely complex. It exhibits nine (if one anthocyanidin is included) out of 13 known primary flavonoid types (Markham 1982), including flavones, flavonols, chalcones, aurones, dihydroflavonols, catechins, dihydrochalcones, flavanones, and anthocyanidins (see Tables 5 and 6). There is no other genus in the *Ericaceae* of comparable size that shows as much flavonoid diversity. In *Rhododendron* (*Ericaceae*), nearly 200 flavonoids (anthocyanidins included) were detected and 33 flavonoids identified for some species by Spethmann (1980). King (1977, 1980) identified more flavonoids from North American *Rhododendron* with 38 flavonoids detected and 28 identified. All types of flavonoid found in *Kalmia* were reported in *Rhododendron* except the aurones. This is the second report of aurones from the *Ericaceae*, the first being from *Vaccinium* by Jankowski and Paré (1983).

The total number of flavonoids isolated from *Kalmia* is 85, of which 76 were isolated in this study (Table 6). Of the 76 flavonoids isolated, 61 are first reports from *Kalmia*. Several of them (at least five) could be new natural products if properly identified using other available techniques, such as mass spectroscopy (m.s.) and nuclear magnetic resonance (n.m.r.) spectroscopy. This was not carried out in the present study because of the complexity of *Kalmia* flavonoids, and financial and time constraints. Fifteen out of 24 previously reported flavonoids (Table 5) were isolated here and the other nine were not detected. Since anthocyanidins were not the focus (floral material was not tested) of this study, the cyanidin-3-O-glucoside presented in Table 5 was ignored. The reason for missing other eight flavonoids is probably due to the fact that those flavonoids are present in only minute quantities and were isolated and identified by natural product phytochemists who would target specific new compounds from specific species and use material several times more than this study used from one species. For example, Dr. Doskotch and his associates used **6.6 Kg** of dried *Kalmia latifolia* leaves for their study (El-Naggar and Doskotch *et al.* 1980; Doskotch 1992, personal communication). Even with this amount of material, they could isolate certain compounds at concentrations just at the limit for the identification purposes, such as kalmiatin, latifolin, and 8-desmethyl-latifolin (Wollenweber 1992, personal communication).

Flavones

Six flavones have been detected in *Kalmia*: four were reported previously by Wollenweber and Kohorst (1981, 1984) as C-methylated flavones (Table 5). Flavones are commonly considered to be more advanced flavonoids compared to flavonols (Harborne 1972). Four flavones were isolated in this study, one of which is a glycoside (Table 6).

C-methylated flavones are rare in nature and their occurrence is sporadic. In seed plants, they have been found mainly in the *Myrtaceae*, and a few other families, such as *Pinaceae*, *Ericaceae*, *Annonaceae*, *Clusiaceae*, and *Fabaceae* (Wollenweber and Jay 1988). In the *Ericaceae*, *Ledum*, and *Gaultheria* have been found to have them besides *Kalmia latifolia*, *K. angustifolia*, and *K. polifolia* (Wollenweber and Jay 1988). The present study adds two more *Kalmia* species to the list, *K. hirsuta* and *K. ericoides*. Except for *K. latifolia*, all four species have two C-methylated flavones, 8-desmethyl-eucalyptin and 8-desmethyl-sideroxylin, which were determined by extended running of PCs, spectral analyses, and comparison with standards provided by Prof. Wollenweber.

In seed plants as a whole, the taxonomic value of C-methylated flavones is not clear (Wollenweber and Jay 1988), but in this study they are of considerable interest. Two *Kalmia* species *K. microphylla* and *K. cuneata* do not show the presence of C-methylated flavones. This might be easier to explain in *K. cuneata* since it is the only deciduous shrub in the genus, and C-methylated flavones have been reported from evergreen plants. On the other hand, *K. microphylla*, which is remarkably similar to, and has been very hard to separate from, *K. polifolia* in every aspect (Table 3), is distinctly different from *K. polifolia* in its absence of the C-methylated flavones. C-methyl-flavones may be a key character in separating these two species. It is also interesting to note that of 58 *K. polifolia* populations, these C-methylated flavones were absent only from four geographic outlier populations. Three are from the northern most part of its range, two from northern Manitoba near Churchill (collections 9028-31, and 9032-36), and another from Cochrane, Ontario (collection 9134). The fourth one is from its southern distribution limit in New Hampshire (collection 9134). This might indicate that C-methylated flavones could be absent due to either genetic drift, or natural selection. It could provide some indication that this species is closely related to *K. microphylla*. *Kalmia angustifolia* also showed a distinct distribution pattern for the C-methyl flavones. Except for one outlier population in the northwest range from Mattice, Ontario (collection 9109), all populations (29) of variety *angustifolia* possess them, while in variety *carolina*, only three of 16 populations have them.

Flavonoid 2.1 (Table 6) was tentatively identified as 8-desmethyl-sideroxylin-5(?)-O-arabinoside and is quite rare in *Kalmia*, found in only ten populations of *K. angustifolia*, two of *K. hirsuta*, and two of *K. ericoides*. This is probably a new natural product. The identification of both the aglycone moiety and sugar moiety of this flavonoid is fairly certain, but the attachment position may need further verification. The time of hydrolysis for this flavonoid was 50 minutes in 1N HCl and the hydrolysis was not quite complete, indicating a strong bound between the two moieties (C- bound?).

Flavonoid 3 (Table 6) was not positively identified. From its spectral and other properties it should be a flavone glycoside. Several hydrolyses were tried on this flavonoid, the longest was 2 hours in 1N HCl and still remained incompletely hydrolysed (C-glycosylation?). It seemed to show the presence of glucose for its sugar moiety. Since this flavonoid has high mobility in AW solvent and is mixed with other unidentified organic compounds its purification is challenging. Another complicating issue is its apparent isomeric chromatographic behaviour. Although its identity is difficult to determine, its presence on PCs is relatively easy to detect because of its unique colour change in ammonia fumes (Table 7). This flavonoid is present in all species, with higher frequencies in *K. angustifolia* (58% of populations), *K. cuneata* (60% of populations), *K. microphylla* (98% of populations), *K. hirsuta* (100% of populations), and *K. polifolia* (100% of populations). All three Cuban mainland populations of *K. ericoides* have rather high concentrations of this flavonoid, while all populations from the Isle of Pines lack it. This indicates a clear geographic divergence in flavonoids between the two regions.

Flavonols

A total of 12 flavonol aglycones have been isolated from *Kalmia*, nine of which were detected in this study. Kaempferol, quercetin-3-O-methyl ether, isorhamnetin, quercetin-3,5,3'-tri-O-methyl ether, myricetin, myricetin-3-O-methyl ether are new reports from this genus (Table 6), whereas kalmiatin, 8-desmethyl-kalmiatin, latifolin, 8-desmethyl-latifolin, quercetin and gossypetin were reported in earlier studies (Table 5).

Of the four C-methylated flavonols, kalmiatin, 8-desmethyl-kalmiatin, latifolin, 8-desmethyl-latifolin, reported only from *K. latifolia* (Wollenweber and Kohorst 1984), only 8-desmethyl-kalmiatin was isolated and characterized in the present study. The remainder are in minute quantities. 8-desmethyl-kalmiatin is found in 98% of the *K. latifolia* populations.

Kaempferol is present in five *Kalmia* species, being most abundant in *K. ericoides* (78% of populations), *K. hirsuta* (100% of populations), and *K. cuneata* (100% of populations). There is little doubt that this is an advanced character for those species (Harborne and Williams 1973; Harborne 1977). Its absence from *K. latifolia* and *K. angustifolia* shows again that these two species are relatively primitive in the genus.

Quercetin (Q) is quite common in angiosperms, and it occurs in 62 percent of dicots, and 28 percent of monocots (Bate-Smith 1962, 1968; Harborne 1967). All *Kalmia* species possess this aglycone. The noticeable differences among the species of *Kalmia* appear to be the different sugar types and their attachment positions among the 12 quercetin glycosides isolated. Attachment positions were found to be 3, 3' or 7. Four diglycosides were detected with the rest being monoglycosides. Galactose, arabinose, and glucose are the common sugars attached to quercetin, and only rarely rhamnose and xylose. The two Q-3'-O-diglycosides (6.11 & 6.12, Table 6) are not on the known flavonoid list (Harborne

1988) and could be new natural products. Q-3-O-galactoside, Q-3-O-arabinopyranoside, Q-3-O-rhamnosylarabinoside, and Q-7-O-glucoside are very common. Flavonoids 6.2 and 6.3 (Table 6) are major glycosides in *K. polifolia* and *K. microphylla*. Upon hydrolysis, both gave quercetin and galactose. They are apparently not hyperin (Q-3-O-galactoside), because they have quite distinct Rfs in several solvent systems on PC and TLC where they were run along with the standard, hyperin. The sugar moiety perhaps has some groups such as an acetyl group attached to it, and more work is needed to establish their full structure. *Kalmia microphylla* shows all the 12 glycosides, followed by *K. polifolia* with eleven, indicating the phylogenetic relatedness of the two species. Q-arabinofuranoside is geographically related in *K. ericoides*, with all populations on Isle of Pines, Cuba being abundant with it, while populations on Cuban main island show no sign of the compound. Again, *K. latifolia* and *K. angustifolia* showed the least variation.

Quercetin-3-O-methyl ether is only found in *K. angustifolia* and *K. cuneata*. It is of interest to note the distribution pattern of this flavonoid in the two varieties of *K. angustifolia*. In var. *angustifolia*, 11 out of 29 populations (38%) were detected having the flavonoid, while in var. *carolina* 15 out of 16 (94%). The spot concentration of this flavonoid on 2-D PCs from var. *carolina* is generally higher than that of var. *angustifolia*. The presence of a 3' position sugar attachment and the sugar xylose, Q-3-O-methyl-3'-O-xyloside, is noteworthy in *K. angustifolia*, because flavonol-3'-glycosylation in this species is rare (7% of populations also have M-3-O-methyl ether 3' xyloside) and it is found in other advanced species in the genus.

Isorhamnetin (Q-3'-O-methyl ether) is found in two species, *K. polifolia* (84% of populations) and *K.*

microphylla (42% of populations). The two common sugars attached to it are galactose and arabinose.

Flavonoid 9 was partially identified. Based on its colour change, spectral data, and its reactions with shift reagents (Table 7), it is a quercetin derivative. The 46 nm bathochromic shift on band I with the addition of NaOMe and NaOAc indicates the presence of a free 4' hydroxy group. No shifts were observed when $AlCl_3$ or $AlCl_3$/HCl were added, indicating the absence of free 3, 5 and 3', 4' hydroxy groups. The 12 nm bathochromic shift on band II with the addition of NaOAc suggests the presence of a free 7 hydroxy group. Therefore this compound is tentatively identified as Q-3,5,3'-tri-O-methyl ether, but a possible identity as Q-3,5,7,3'-tetra-O-methyl ether can not be ruled out completely. The first flavonoid is not reported in the literature of known flavonoids, but the second was reported from *Astragalus centralpinus* (*Fabaceae*) (Wollenweber and Jay 1988). The reported Q-3,5,7,3'-tetra-methyl ether was not available for comparison. Flavonoid 9 is found in all *Kalmia* species except *K. cuneata*.

Gossypetin (G) is conceivably formed by the oxygenation in the 8-position of quercetin as its precursor molecule (Wong 1976). In angiosperms it is of polyphyletic origin since it occurs in a number of unrelated families (Harborne and Turner, 1984). This compound is of considerable taxonomic interest at subfamilial and generic levels in four families, the *Ericaceae*, *Empetraceae*, *Asteraceae*, and *Primulaceae*. In the *Ericaceae*, it is almost entirely confined to the tribes *Rhodoreae* and *Phyllodoceae* (Harborne and Williams 1973), and it was regarded as a primitive biochemical relict in the family *Ericaceae* (Harborne 1977). Harborne (1977) mentioned that gossypetin in the genus *Rhododendron* is strikingly correlated with the general geographical evolution. He believed that *Rhododendron* originated in the Himalaya and north (he meant south?) west China, and considered the distribution of gossypetin supports this. It was present in 76% of Chinese species and only 12% of the species in Malaysia and New Guinea. Gossypetin was first reported in *Kalmia latifolia* and *K. angustifolia* by Harborne and Williams (1969, then 1973). Most often, the sugar, galactose is attached to gossypetin as G-3-O-galactoside. In this study, another monoglycoside (10.2, Table 6) was isolated, but the sugar identity was not established due to the low concentrations of the compound. The distribution of gossypetin in *Kalmia* is not universal, being present in 180 out of 248 populations (73%). It is not detected in *K. cuneata* and is found in only one out of 25 populations (4%) in *K. hirsuta*. To some extent, this study confirms Harborne's hypothesis, since *K. hirsuta* and *K. cuneata* are considered as advanced species of *Kalmia* (Southall and Hardin 1974). On the other hand, the hypothesis is hard to justify when we consider the gossypetin distribution in other *Kalmia* species, especially *K. latifolia* (43% of populations), *K. polifolia* (98% of populations), and *K. microphylla* (97% of populations), since we can hardly consider the latter two species as primitive in *Kalmia*. This is also true with respect to the distribution of myricetin in *Kalmia*, which will be discussed next. The individual seasonal flavonoid variation study of *K. polifolia* carried out in the summer of 1992 (unpubl. data) indicates that this flavonoid is not persistent in all individuals throughout the growing season, the highest concentration appeared to be at the budding stage in late August, while the lowest concentration was observed at fruiting stage in June. Some individuals showed no sign of gossypetin in June sampling.

Myricetin (M), like gossypetin, is regarded as a primitive flavonoid because it has been shown to be abundant in woody plants, especially primitive woody plants (Bate-Smith 1962, 1968; Harborne 1969, 1972, 1977). Bate-Smith (1962) considered that B-ring trihydroxy flavonoids (such as myricetin) arise from non-aromatic precursors by a route quite different from that by which the mono- (like kaempferol) and dihydric (like quercetin) constituents are formed. For b (trihydroxy present) → b_o (trihydroxy absent) to be a reversible process, would require the creation *de novo* of the enzyme system responsible for this synthesis in any evolutionary line from which it had been lost. He concluded that b → b_o is an irreversible process, and that the trend in evolution from the earliest emergence of the dicotyledons has always been in the direction b → b_o. In *Kalmia*, myricetin is found only in three species *K. polifolia*, *K. microphylla*, and *K. hirsuta* with 100% of populations in each species. Since one can hardly consider them as primitive in *Kalmia* (Southall and Hardin 1974), the presence of myricetin in them should be judged differently. It can be argued that the probable ancestor, *K. latifolia* or its closely related taxon, had myricetin earlier and it lost the compound after it gave rise to other species. Or, myricetin was absent from *K. latifolia* and it was acquired by the three descendants. The latter seems more probable and hence I regard the presence of myricetin as an advanced character within *Kalmia*. The distribution of this aglycone also unites the decussate leaved shrubs of *K. polifolia* and *K. microphylla* together with the hairy alternate leaved *K. hirsuta*. This may seem controversial first, but may reflect the true phylogeny of this genus after the discovery of two *K. hirsuta* populations, one in Georgia (collection 9184), and the other in Florida (9199). The Georgia population was collected in an open area of a pine forest where *K. hirsuta* can be found in both open areas and somewhat shaded areas. The individuals in open areas look like typical *K. hirsuta* with pubescent surfaces, while some individuals in shaded areas show almost completely glabrous leaves, which resemble *K. microphylla* (in fact, my assistant Kevin shouted "*polifolia*" when he saw the plant). The Florida population was collected on a road side and almost all plants of *K. hirsuta* were glabrous. Within the three species, differences exist in the glycosylation pattern. The dominant myricetin glycoside in *K. hirsuta* is M-3-O-rhamnoside (96% of populations), followed by M-3-O-arabinopyranoside (76% of populations) shared with *K. microphylla* (83% of population), and M-3-O-galactoside (64% of populations) shared with *K. polifolia* (100% of populations) and *K. microphylla* (100% of populations). *Kalmia polifolia* and *K. microphylla* show their close relatedness again by both having M-3-O-glucoside, M-3-O-arabinofuranoside, M-3'-O-glucoside, and M-3'-O-xyloside. Flavonoid 11.8 (Table 6) is partially identified. Hydrolysis gave myricetin and xylose, and it is possibly M-5'-O-xyloside, found only in *K. polifolia*.

Myricetin-3-O-methyl ether has a sporadic distribution in three species, *K. angustifolia* (7% of populations), *K. microphylla* (23% of populations), and *K. polifolia* (76% of populations). Three populations of *K. angustifolia* with the flavonoid were all var. *carolina*. In *K. microphylla*, this aglycone distribution seems to be correlated with the distribution of dihydrochalcones (see discussion there). *Kalmia polifolia* specimens do not seem to show any geographic pattern for this flavonoid, but this aglycone is a major flavonoid constituent in its stem and root organs (unpubl. data). Myricetin-3-O-methyl-3'-O-xyloside is found in all three species. Flavonoid 12.2 (Table 6) is found in *K. polifolia* and *K. microphylla*, and it gave M-3-O-methyl ether and two sugars, glucose and xylose, upon hydrolysis. Though the sequential attachment has not been established, it is not reported in the literature of known flavonoids whatever the sequence would be, glucosylxyloside or xylosylglucoside.

Three flavonols remain unidentified, all of which are glycosides (Ufg.), Ufg.1-3. All were found in *K. polifolia* and *K. microphylla*, Ufg.1 also in *K. angustifolia* and *K. cuneata*, Ufg.3 in *K. cuneata*, *K. ericoides*, and *K. hirsuta*.

Chalcones

Chalcones are precursors of all other flavonoids and therefore should be regarded as ubiquitous compounds in the plant kingdom (Swain 1976; Wong 1976). They are commonly undetectable since they are the presumed biosynthetic intermediates of other flavonoids. On rare occasions they accumulate in plant tissues and become detectable (Swain 1976; Wong 1976). So it is generally agreed that biosynthetically they represent the most primitive flavonoids. They have been found in ferns and several primitive angiosperm families (Harborne 1977; but see Bohm 1988). Structurally, none of the flavonoids of this type were fully identified in this study. Based on their colour and spectral data, they were tentatively identified as chalcones. They are only found in *K. latifolia* and *K. angustifolia*, which are considered to be relatively primitive. More work needs to be done on chalcones in *Kalmia*.

Aurones

Aurones are the products of enzyme oxidation of chalcones, which is considered to be an evolutionary advancement. In *Kalmia*, two aurone aglycones were isolated. Though their identities are not fully established, their identity as aurones seems to be quite reliable according to the available data (Table 7). They are especially conspicuous when viewed under the UV light and they are bright yellow in colour in daylight.

Flavonoid 16 (Table 6), is one of the two aurone aglycones, aurone #1. Two glycosides of this aglycone were isolated based on rhamnoside and glucoside. Aurone #1 is distributed in three species, *K. latifolia* (100% of populations), *K. angustifolia* (49% of populations), and *K. microphylla* (30% of populations, Fig. 4). Mountain laurel (*K. latifolia*) is unique as it possesses both glucosides of this aglycone, while the other two species have the rhamnoside only. As it has been shown, *K. latifolia* and *K. angustifolia* are very closely related, so this occurrence comes as no surprise. The appearance of aurone #1 in *K. microphylla* deserves a comment. All populations possessing this aglycone are from the Pacific lowland area from Washington to Alaska, where the entity *K. occidentalis* was traditionally treated either as *K. polifolia* or as a subspecific taxon under *K. polifolia* or *K. microphylla* (see Table 3). The plants from the lowland area are usually taller and have leaves that are very similar to typical "polifolia" form, and they appear to represent the ancestral populations of *K. microphylla* (also see discussion under dihydrochalcones, Fig. 4). Geographically, *K. latifolia* and *K. angustifolia* are on the east side of the continent while *K. microphylla* is on the west. *Kalmia microphylla* could have acquired the aurone and dihydrochalcones from its probable ancestor *K. latifolia* or its closely related taxon. This matter will be explored in the next chapter.

The second aurone aglycone, aurone #2, has three glycosides, but none of them were identified for the sugar moiety because of low concentrations. Although it is a rather weak leaf constituent, its fluorescent greenish colour is not hard to detect. Except for *K. microphylla* and

K. ericoides, all other species have this aglycone. It is abundant in *K. polifolia* which is the only species having all three glycosides of aurone #2. The remaining four species have the same glycoside 17.3 (Table 6). It is surprising that this aglycone is absent from *K. microphylla* which has aurone #1. In an independent study of *K. polifolia*, it was found that this aurone shows not only seasonal variation but also the organ specificity, the highest concentration is found in the root systems (unpubl. data). It is interesting to note that the distribution of aurones mirrors the C-methylated flavone distributions, which set *K. polifolia* and *K. microphylla* apart.

Dihydroflavonols

Dihydroflavonols are very common in *Rhododendroideae* (Harborne and Williams 1973) and are considered as primitive characters (Harborne 1977). Only one kind of aglycone, taxifolin (T) (dihydroquercetin) was found in *Kalmia* with two glycosides, T-3-O-glucoside and T-3-O-xyloside. This is the first report of a dihydroflavonol from *Kalmia*. Taxifolin commonly occurs in its glycoside form, the isolation of its free aglycone form (18, Table 6) was probably the result of degradations during the process of drying or isolation. It is considered to be the precursor of the flavonol, quercetin, and can be easily oxidized (Wong 1976). Indeed, it was shown in an independent study that only the young leaves of *K. polifolia* in June and July have relatively high concentrations of this aglycone. As the leaves age, this flavonoid disappears gradually (unpubl. data). This aglycone is found in *K. polifolia* and *K. microphylla*. In *K. microphylla*, it seems to follow the geographic distribution of dihydrochalcones (see discussion there, Fig. 4).

Catechin

Catechin belongs to the flavan-3-ols class of flavonoids and is widespread in angiosperms like the flavonol quercetin (Porter 1988). Therefore it is not surprising that it is found in all *Kalmia* species.

Dihydrochalcones

Dihydrochalcones should be considered biochemically primitive in *Rhododendroideae*, and they were reported from *Rhododendron* (King 1977, 1980; Mabry *et al.* 1975). Dihydrochalcones in *Kalmia* have been known for some time (Table 5, Bohm 1988). So far five aglycones have been reported with four of them being isolated in this study. Flavonoid 23 (Table 6) was partially identified and could be a new compound. Flavonoid 22, asebogenin, was identified by comparison with published spectral data and other properties such as colour changes (Mabry *et al.* 1975). Flavonoids 20, 20.1, 20.2, 21, and 21.1 (Table 6) were compared with the standards provided by Prof. Doskotch. Flavonoid 22.1 (Table 6) gave asebogenin and glucose upon hydrolysis and is identified as asebotin (asebogenin-2'-O-glucoside) which was already reported from *Kalmia* (Table 5). Flavonoid 22.2 (Table 6) was identified as asebogenin-2'((?)-O-galactosylxyloside, the sequence of the sugars was not established, and attachment position is tentatively assigned at 2' position. It is also probably a new compound.

Phloretin is found in *K. latifolia* (100% of populations) and *K. microphylla* (18% of populations), showing the similar geographic distribution pattern of aurone #1 (flavonoid 16). Again, the populations showing phloretin in *K. microphylla* are restricted to the Pacific lowland area from Washington to Alaska. This will be discussed below.

3-hydroxy-phloretin is found only in *K. latifolia* (100% of populations), showing some specialization by adding a hydroxy group to phloretin in dihydrochalcones.

Asebogenin (A) has a wider geographic distribution, all populations of *K. latifolia*, *K. angustifolia*, *K. hirsuta*, and *K. ericoides* have this aglycone. Fifty six percent of the *K. microphylla* populations showed the presence of this flavonoid. The major form is A-2'-O-galactosylxyloside in *K. latifolia* (93% of populations), while asebotin is only found in 20 percent of the populations. *Kalmia angustifolia* has almost equal distributions, among populations, for asebotin and A-2'-O-galactosylxyloside, 69 percent and 76 percent respectively. It appears that the former is commonly found in var. *angustifolia* (100% populations, only 13% of populations in var. *carolina*), and the latter in var. *carolina* (100% of populations, 66% of populations in var. *angustifolia*). The earlier report by Williams (1964) that *K. latifolia* has phloridzin whereas *K. angustifolia* has only asebotin seems unfounded and seemingly cannot be used to separate the two species.

The distribution of dihydrochalcones in *K. microphylla* is especially interesting. The present distribution of this species covers basically the Rocky Mountains and western Coastal Mountains of North America. It is also found in the Pacific lowland from Washington to Alaska, and the northern part of Canada west of Hudson Bay. Taking historical events into consideration, mapping the distributions of dihydrochalcones along with aurone #1, flavanone #3, and a dihydroflavonol (taxifolin) (Table 6), it appears that the geographic distributions of those relatively primitive flavonoids are correlated with the unglaciated areas, and unglaciated corridors (Fig. 4). Flavanone #3 (flavonoid 26)

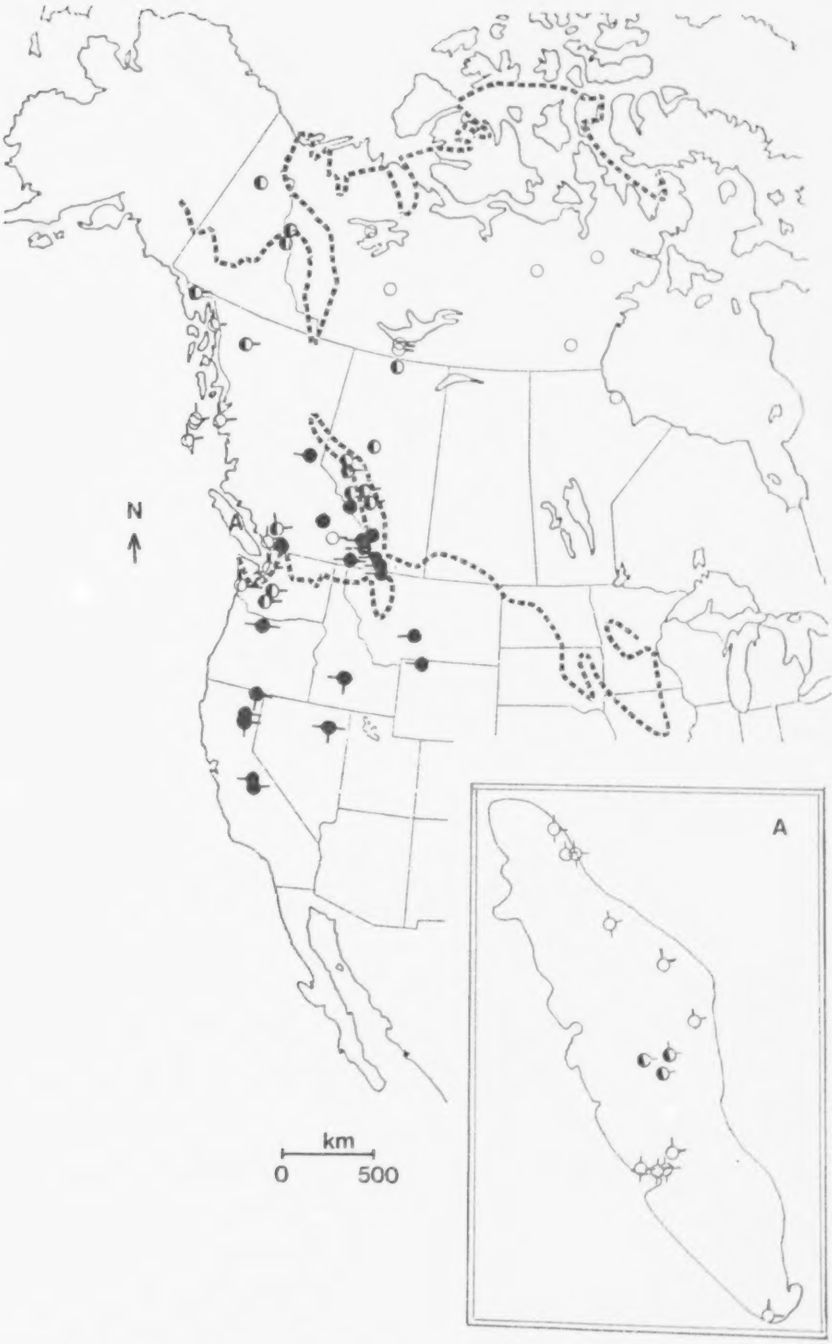

Figure 4. Map of North America, showing the distribution of Dihydrochalcones (- right), Aurone #1 (- top), Taxifolin (- bottom), and Flavanone (agl.3) (- left) in *Kalmia microphylla*. Circles: hollow = elevation below 3000'; half filled = 3000-5000'; filled = above 5000'. The approximate Wisconsin glacial maximum, following Prest (1984), is indicated by the dotted lines. Insert A = Vancouver Island.

is found in populations from higher elevations. It is my opinion that the ancestral populations of *K.microphylla* were quite like the present Pacific lowland entity, and could be referred to as chemotype "occidentalis". This taxon may have survived the Pleistocene glaciations just south of the glaciers or in the unglaciated corridors. The most ancestral populations could be identified as those plants which are found in the Vancouver and adjacent Washington lowland areas, Queen Charlotte Islands, and Vancouver Islands because of their distinct flavonoid profiles (Tables 8 and 9). I would dismiss the hypothesis that the lowland entity "polifolia" hybridizes with entity "microphylla" producing an intermediate type (Hitchcock *et al.* 1959). I regard the whole situation as progressive advancements of the ancestral populations to areas vacated by the ice-sheets. As the plants were spreading to suitable habitats and occupying higher elevations, they lost the primitive flavonoids and gained some new flavonoids such as flavonoid 26 (Table 6) in the process. The analysis of all populations will be done in analysis 4, and further reference to this will be made in the next chapter.

Flavanones

Flavanones are isomers of chalcones catalyzed by isomerases inside the plant tissues, and their function in the flavonoid biosynthetic pathway is not well understood (Wong 1976). Three aglycones were isolated and partially characterized in this study. Flavonoid 24 (Table 6) is rather common, found in all species except *K. latifolia*. Two glycosides of the flavonoid 25 (Table 6) were isolated and both were found only in *K. angustifolia*, and especially abundant in the var. *carolina* (Appendix 2). Flavonoid 26 (flavanone #3) (Table 6) is only found in its aglycone form and found in *K. ericoides* (89% of populations) and *K.*

microphylla (20% of populations). All populations of *K. microphylla* having the flavonoid are from high elevations (Fig. 4).

In summary, *Kalmia* shows a complicated flavonoid profile. One should be cautious in trying to interpret the systematic implications of certain flavonoids because what are generally regarded as primitive flavonoids may be advanced characters in some *Kalmia*. Such flavonoids are myricetin and taxifolin. The overall systematic and phylogenetic implications of flavonoid profiles in all populations of *Kalmia* will be presented below.

B. Numerical Analyses[1]

All characters used in the analyses are flavonoid characters, and flavonoid profiles of 248 populations are presented in Appendix 2. Flavonoid profiles for each species are presented in Appendix 3. Since the results of cluster analyses 1 to 4 are just smaller subsets of analysis 5, except for the cophenetic correlation coefficients (matrix correlation), their individual results will be presented in Appendix 5 for reference, and only a condensed phenogram is presented in Fig. 9 (see discussion under analysis 5).

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[1] Here I would like to outline my perception of infraspecific category usages. Although one is allowed to use up to five infraspecific categories, including subspecies, variety, subvariety, form, and subform (Greuter *et al.* 1988), only three of those are commonly used, subspecies, variety, and form (Stuessy 1990). One point that is baffling is the confusing usages of subspecies and variety. Even though one can define the differences between the two (see Stuessy 1990, Table 12.1, p. 189), in practice it is very hard to follow. It appears that certain taxonomists favour one category over another in various floristic works. In this study, I would like to continue the established practice in this genus, i.e. to recognize the infraspecific category at the varietal level (Tables 2-4).

Analysis 1. *Kalmia angustifolia - carolina*

A total of 45 populations were scored for the 34 flavonoids isolated from this complex. The results of cluster analyses are presented in Fig. 9 and Appendix 5, A with the matrix correlation being 0.8648. The result of PCA is presented in Fig. 5. From the above analyses, it is clear that this complex segregates into two easily recognizable groups, entities *angustifolia* and *carolina*. Although they are separated easily based on flavonoid analyses, I am somewhat reluctant to recognize them at specific level, because there is really no reliable morphological features separating them, as indicated by Ebinger (1974). I advocate keeping them at the variety level, that is, *K. angustifolia* var.*angustifolia* and *K. angustifolia* var. *carolina*. There are several flavonoids showing distinct distributions among the two varieties, such as C-methylated flavones (97% of populations in var. *angustifolia*, and 19% of populations in var. *carolina*), Q-3-O-methyl ether (38% of populations in var. *angustifolia*, and 94% of populations in var. *carolina*), and asebogenin glycosides as discussed earlier. None of them, however, is consistently present in one variety or absent from another. A noticeable phenomenon in this species is that it has the highest number of flavonoid aglycones (18 out of 26) in the genus, and the PCA graph shows that both varieties have considerable variation among the populations, which agrees in general with the degree of morphological variation already noted from earlier observations (Ebinger 1974; also my own observations). The disjunct distribution of the var. *carolina* is obvious, and genetic exchange would have been hindered by that, which is well reflected here by interpopulation flavonoid differences (Appendix 2).

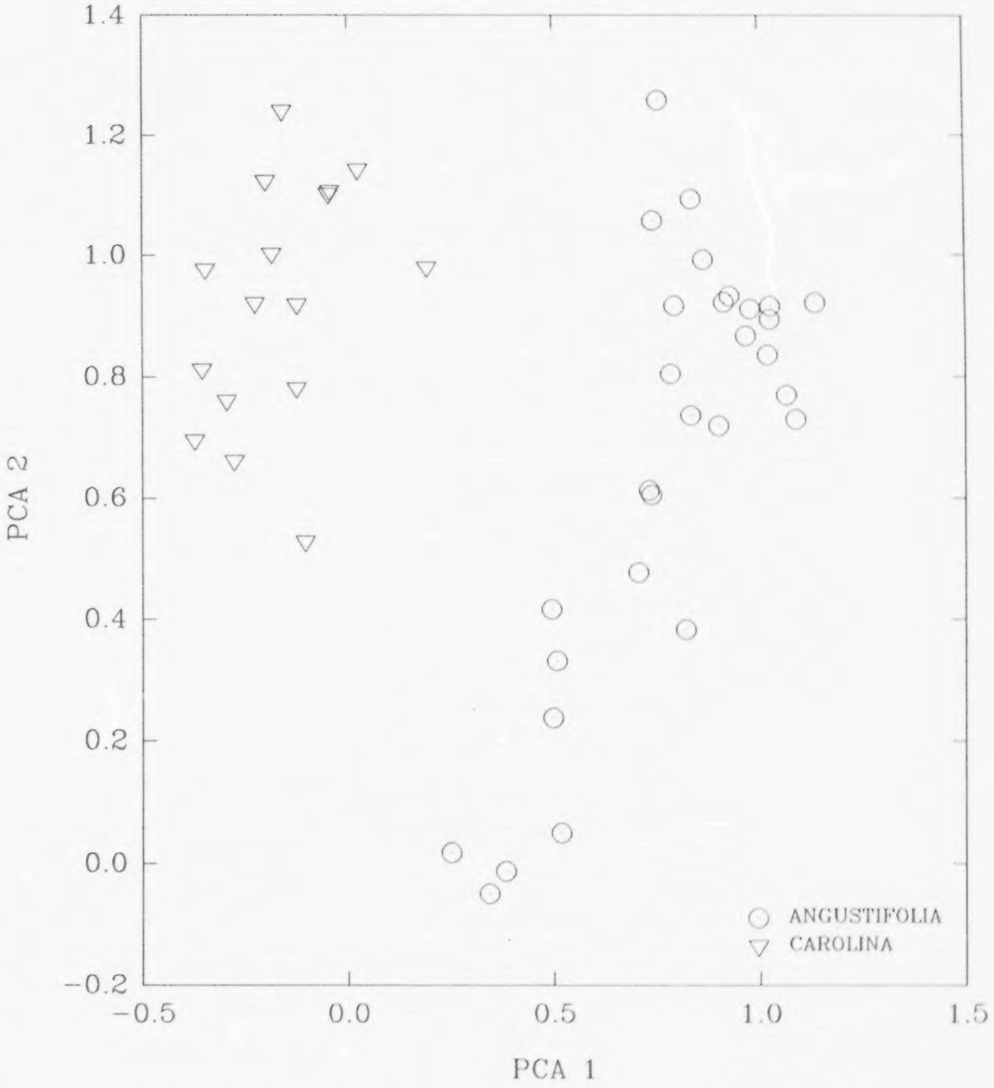

Figure 5. PCA of two varieties of *Kalmia angustifolia* based on flavonoid characters (Appendix 2). PCA 1 represents 27.42%, and PCA 2 14.54% of the variation.

Analysis 2. *Kalmia ericoides* and *K. hirsuta*

It appears that all previous revisions of *Kalmia* assumed that *K. hirsuta* and *K. ericoides* are distinct taxa, because they are separated geographically, one on mainland North America and the other on the Cuban islands. Much effort was taken to clarify the status of the Cuban species (Table 4). This analysis contains 34 populations (*K. hirsuta* 25, *K. ericoides* 9) and involves 13 aglycones and a total of 32 flavonoids. The results of cluster analyses are presented in Fig. 9 and Appendix 5, B and the matrix correlation is 0.9579. The result of PCA is presented in Fig. 6. From the phenograms (Fig. 9, and Appendix 5, B), it is interesting to note that populations of *K. ericoides* are intermingled with the populations of *K. hirsuta*. Though *K. hirsuta* populations are still aggregated, the Cuban populations especially the Cuban main island populations ("E-eri" in Fig. 9, "EVE" in Appendix 5, B) do not separate from this group. The result of PCA clearly shows that the PCA 1 separates *K. hirsuta* (⊙) from *K. ericoides*, and the PCA 2 divides *K. ericoides* into two groups, "□" group and "▽" group. *Kalmia hirsuta* is apparently distinct but very closely related to *K. ericoides*. Southall and Hardin (1974), and Borhidi (1985) considered *K. hirsuta* to be the ancestor of *K. ericoides*, which is supported by this analysis. The Cuban entities are closely related, and it might be appropriate to treat them as a single species. The two separated groups could be recognized at variety level, *K. ericoides* var. *ericoides* (▽) and var. *aggregata* (□). They are separate geographically and show distinct flavonoid profiles, the former with flavonoid 3 and without flavonoid 6.5 (Table 6), while the latter just the opposite. The results support the revision by Judd (1983), and disagree with other recent revisions (Ebinger 1974; Southall and Hardin 1974; Berazain and Sorribes 1987;

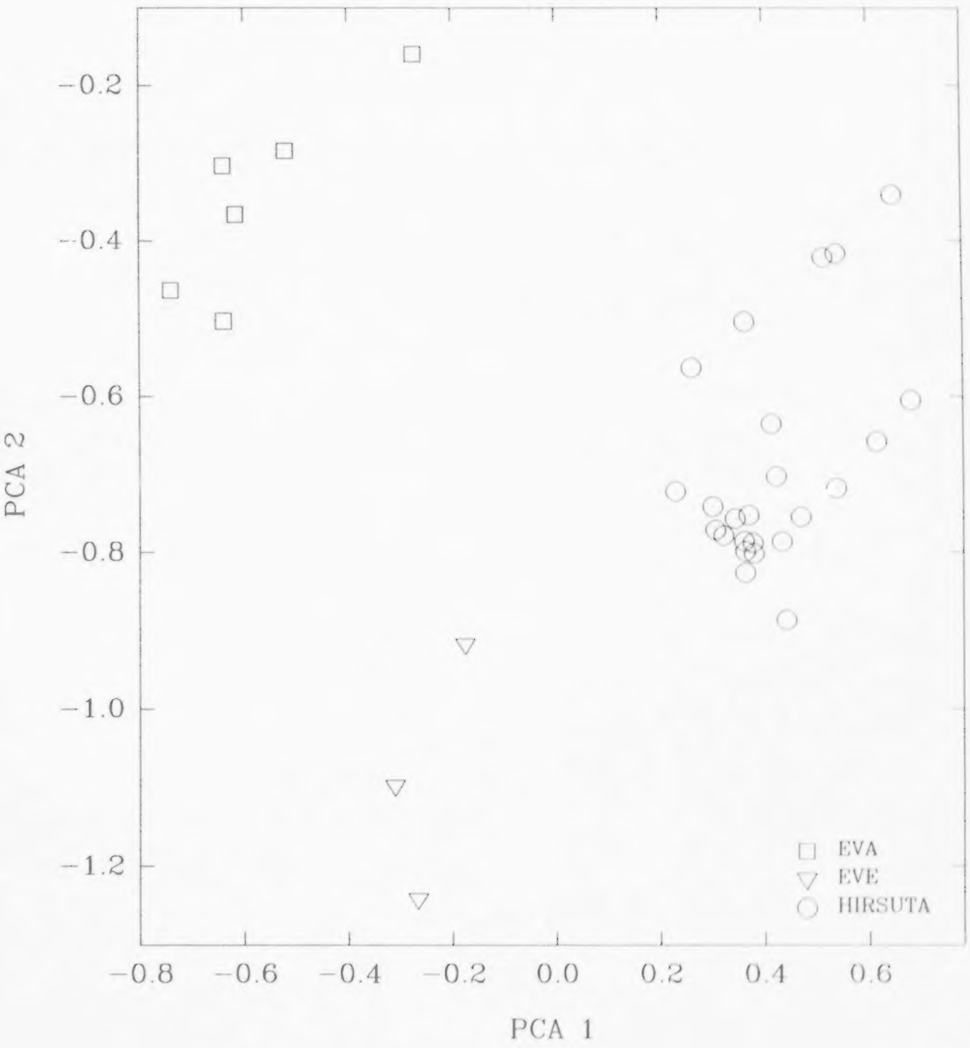

Figure 6. PCA of *Kalmia ericoides* and *K. hirsuta* based on flavonoid characters (Appendix 2). PCA 1 accounts for 31.70%, and PCA 2 12.11% of the variation.

(EVA = *K. ericoides* var. *aggregata*; EVE = *K. ericoides* var. *ericoides*).

see Table 4). If the hypothesis that *K. hirsuta* is the ancestor of *K. ericoides* is accepted, then the ancestral populations must have migrated to the mainland Cuba first, losing the aglycone myricetin, and further to the Isle of Pines during the last glaciation. In this process flavonoid 3 (Table 6) was lost. Phytogeographic implications will be the topic of the next chapter.

Analysis 3. *Kalmia polifolia* and *K. microphylla*

The *Kalmia polifolia - microphylla* complex has puzzled and divided taxonomists for more than a century. Even after two recent revisions (Ebinger 1974; Southall and Hardin 1974), the issue has not been resolved (Table 3). The present analysis contains 124 populations sampled from the entire natural range (Fig. 18). Each population was scored for 57 flavonoids isolated from the complex. The results of cluster analyses are presented in Fig. 9 and Appendix 5, C with the matrix correlation being 0.8230. The result of PCA is presented in Fig. 7. In Fig. 7, the taxa were classified according to Ebinger's treatment (1974). The results of both cluster and PCA analyses distinctly separate *K. polifolia* and *K. microphylla*. The most important aspect of the analyses is that the group *K. microphylla* var. *occidentalis* (⊙), which has been treated by many as "*K. polifolia* (□)" (Table 3), is clearly different from *K. polifolia*. They are well separated in the cluster analyses (Fig. 9, and Appendix 5, C) and on PCA 1 (Fig. 7). It seems best to separate the populations into two distinct species *K. polifolia* (□) and *K. microphylla* (∇ & ⊙), which is supported by flavonoid chemistry, cytology (Jaynes 1969), morphology (Ebinger 1974), and geographic separation (Fig. 18). The infraspecific treatment of *K. microphylla* will be dealt with in the next analysis.

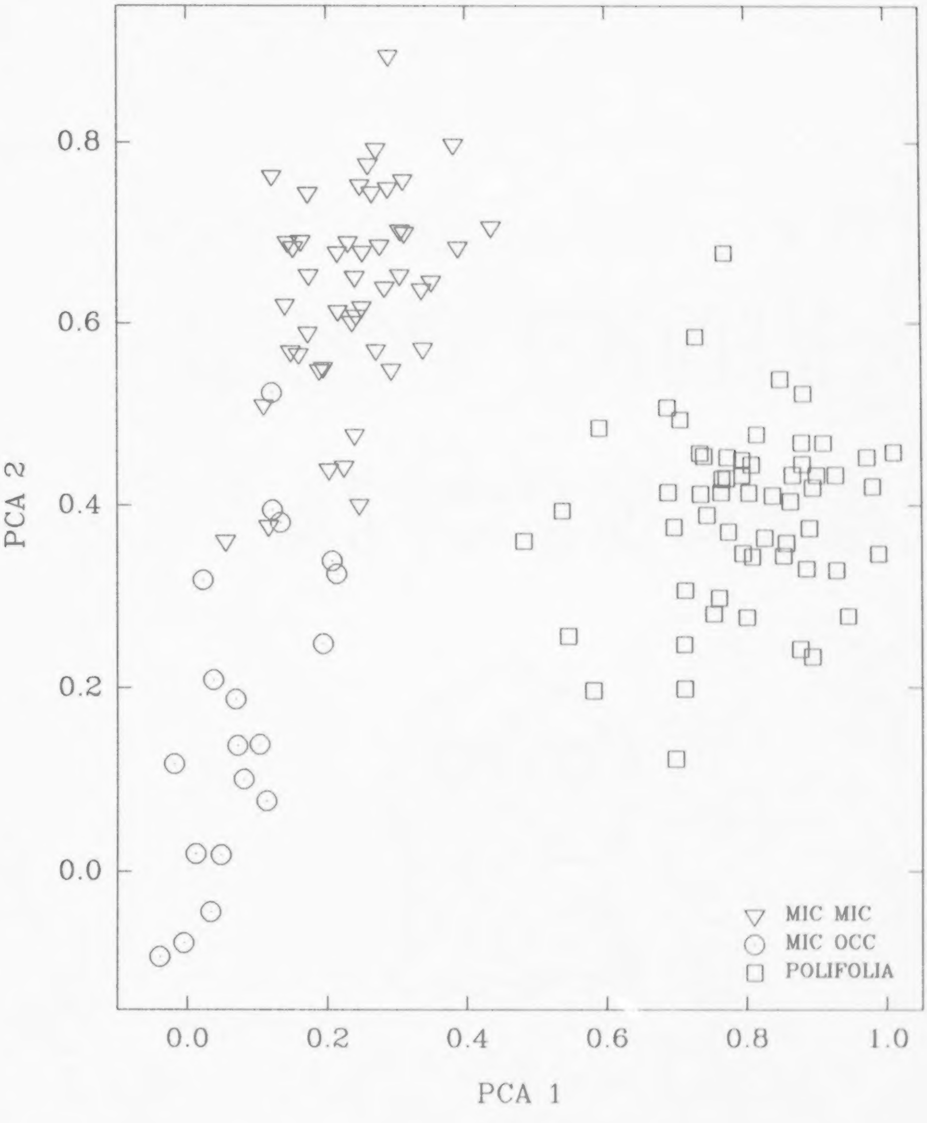

Figure 7. PCA of *Kalmia polifolia* and *K. microphylla* (MIC) based on flavonoid characters (Appendix 2). PCA 1 represents 21.57%, and PCA 2 10.13% of the variation.

(Entities MIC = *K. microphylla*; OCC = *K. occidentalis*)

Analysis 4. *Kalmia microphylla*

A total of 66 populations were scored for 47 flavonoids in this analysis. The results of the cluster analyses are presented in Fig. 9 and Appendix 5, D with the matrix correlation being 0.7459. The result of PCA is presented in Fig. 8. In the phenograms, the populations with "M-mic" symbols (Fig. 9) or without "*" symbols (Appendix 5, D) are those that were identified morphologically as *K. microphylla* var. *microphylla*, "M-occ" (Fig. 9) or "*" (Appendix 5, D) as *K. microphylla* var. *occidentalis* (Ebinger 1974). It is apparent that populations do not form two cohesive groups corresponding to the current morphological circumscriptions, rather that populations from the Vancouver area form a fairly distinct cluster irrespective of morphology (Fig. 9, and Appendix 5, D). Fig. 8 shows a somewhat similar picture, in which populations are separated weakly. There are indications that PCA 1 separates the two entities (▽ and ⊙) and one might argue that this should be sufficient to recognize them as varieties or subspecies. I am reluctant to do so at present because it is very difficult to identify specimens from the west coast using morphology, especially those with intermediate features. The difficulty in separating the two entities was noted in several regional floras that identified them as intergrades (Hitchcock *et al.* 1959; Wallace 1993). In my judgement that all populations should be treated as a single variable species with two chemotypes, "*occidentalis*" with dihydrochalcones and aurone #1, and "*microphylla*", without them. There is not a strong discontinuum separating the two chemotypes, rather there is a gradual transition from those with to those without the dihydrochalcones and aurone #1, i.e. a "chemocline" (Fig. 4).

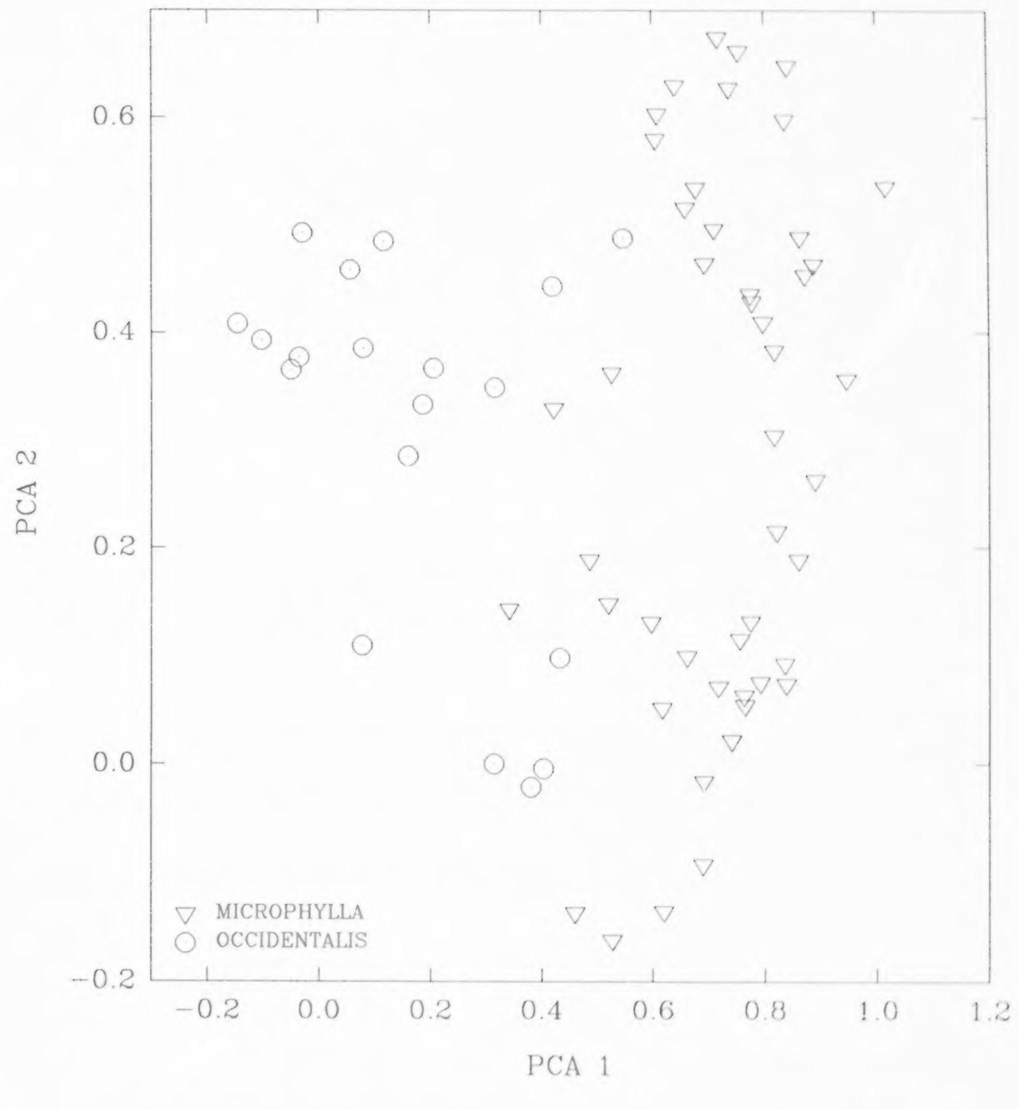

Figure 8. PCA of *Kalmia microphylla* based on flavonoid characters (Appendix 2). PCA 1 accounts for 20.71%, and PCA 2 11.89% of the variation.

Analysis 5. The genus *Kalmia*, all populations[2]

All *Kalmia* populations, 248 in total, were included in this analysis with 76 flavonoids being scored for each population. The result of cluster analysis is presented in Fig. 9, with the matrix correlation being 0.9996. The original phenogram shows the relationships of all populations except two *K. hirsuta* populations (9186 and 9187) which aggregate into a single unresolved branch. In order to reduce space, a condensed version is presented here (Fig. 9), that is, the scale was changed from the original 0 - 1.5 to the present 0.5 - 1.5, while the number of operational taxonomic units (OTUs) was reduced from the original 247 to the present 76. This was obtained through an arbitrary scale setting in NTSYS analysis (TREEG) and the printout phenogram was used as a guide in the manual handling of the tree file which was treated by replacing population names with species symbols, and reducing the number of corresponding terminal parameters. The result of PCA is presented in Fig. 10. The results distinguish seven species well except for *K. hirsuta* and *K. ericoides* which were already shown to be chemically distinct in analysis 2. There is little doubt that *K. latifolia* is very distinct from other species as is shown by both the phenogram and the PCA (Figs. 9 and 10). *Kalmia latifolia* itself, on the other

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2. For comparison, a binary data set was obtained from Appendix 2 by converting all the numbers "2 & 3" into the number "1". The binary data set, the same size as analysis 5, was analyzed using the same programs. The resultant phenogram is comparable to that of Fig. 9 at the specific and varietal levels, except that the "E-eri" populations (Fig. 9) are grouped together next to "E-agg" populations. As in Fig. 9, the populations of *Kalmia microphylla* are not divided into two recognizable entities, *microphylla* and *occidentalis* (in fact, they intermingle further with each other).

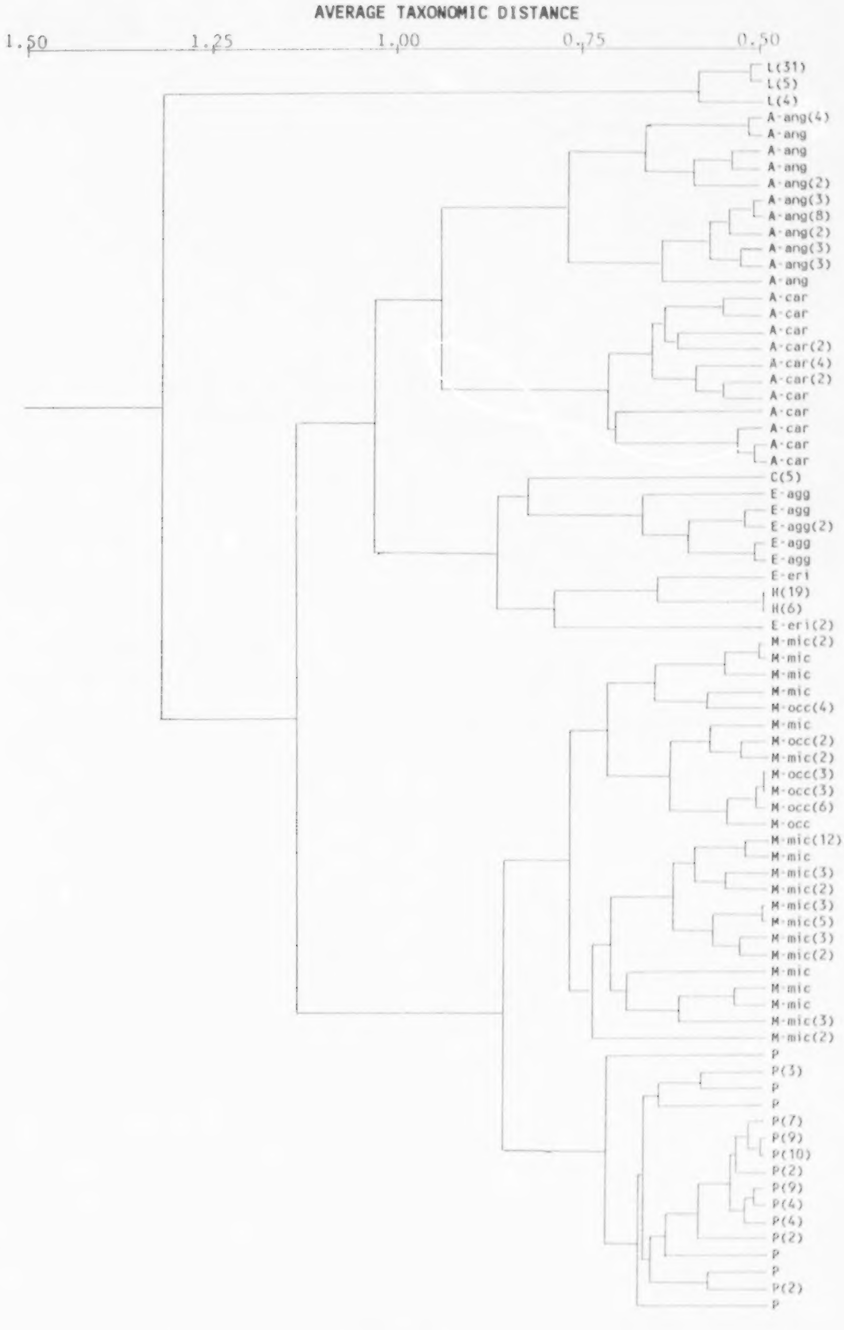


Figure 9. Cluster analysis of all *Kalmia* populations based on flavonoid characters (Appendix 2).

A = *K. angustifolia* (ang = var. *angustifolia*, car = var. *carolina*); C = *K. cuneata*; E = *K. ericoides* (agg = var. *aggregata*, eri = var. *ericoides*); H = *K. hirsuta*; L = *latifolia*; M = *K. microphylla* (mic = entity *microphylla*; occ = entity *occidentalis*); P = *K. polifolia*. The number in parenthesis is the number of populations included at the terminal. Letter(s) alone, one population.

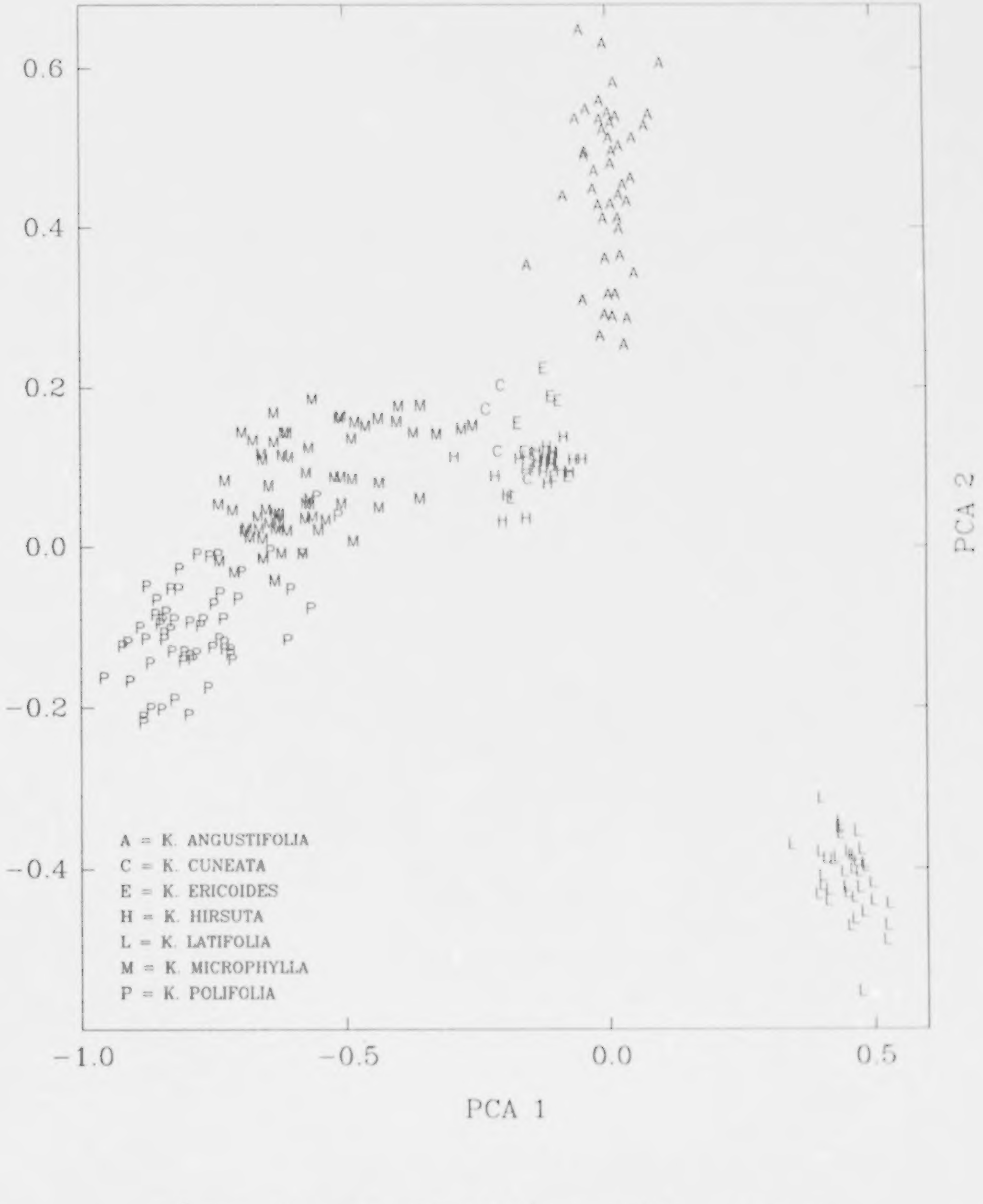


Figure 10. PCA of *Kalmia* species based on flavonoid characters (Appendix 2). PCA 1 represents 27.26%, and PCA 2 12.48% of the variation.

hand, is rather uniform in term of flavonoid profiles with no indication of the need for infraspecific entities. *Kalmia cuneata* shows the least flavonoid variation followed by *K. hirsuta* and *K. latifolia*, while *K. angustifolia* is the most variable species. The close relationship between *K. cuneata* and *K. ericoides* var. *aggregata* is explained by parallel flavonoid reductions rather than phylogenetic affinity if we accept that *K. hirsuta* is the ancestor of *K. ericoides s.l.* The relationships among other species have been dealt with in the previous analyses.

Analysis 6. The genus *Kalmia*, all species

The usefulness of flavonoid aglycones alone in distinguishing the *Kalmia* species is explored in this analysis. The seven OTU's (species) were chosen as the results of the previous analyses and scored for 24 flavonoid aglycones (aglycones 15 and 23 in Table 9 were dropped due to the difficulty of determining their scores). The percentages of flavonoid aglycone distribution (Appendix 3) were used in this analysis. The result of the cluster analysis is presented in Fig. 11 with the matrix correlation being 0.8072. The result of PCA is presented in Fig. 12. Both results separate the seven species of *Kalmia*. The close relationships between the two pairs, *K. angustifolia* and *K. latifolia*, *K. polifolia* and *K. microphylla* are apparent on the phenogram. *Kalmia hirsuta* is closely related to *K. ericoides* and *K. microphylla* in PCA (Fig. 12). The implication of the close relationships among *K. hirsuta*, *K. microphylla*, and *K. polifolia* (Figs 11 and 12) will be discussed in next section. Again, the similarity between *K. ericoides* and *K. cuneata* is regarded as parallel flavonoid reductions.

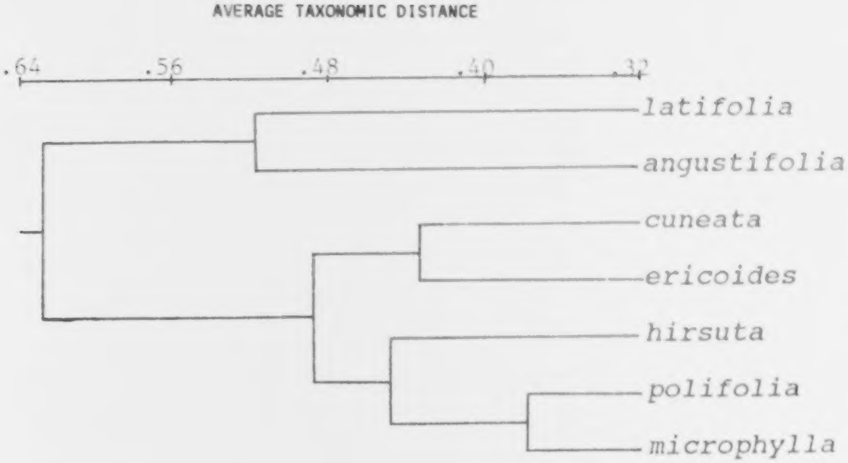

AVERAGE TAXONOMIC DISTANCE
.64
.56
.48
.40
.32
latifolia
angustifolia
cuneata
ericoides
hirsuta
polifolia
microphylla

Figure 11. Cluster analysis of *Kalmia* species based on flavonoid aglycone characters (Appendix 3, II).

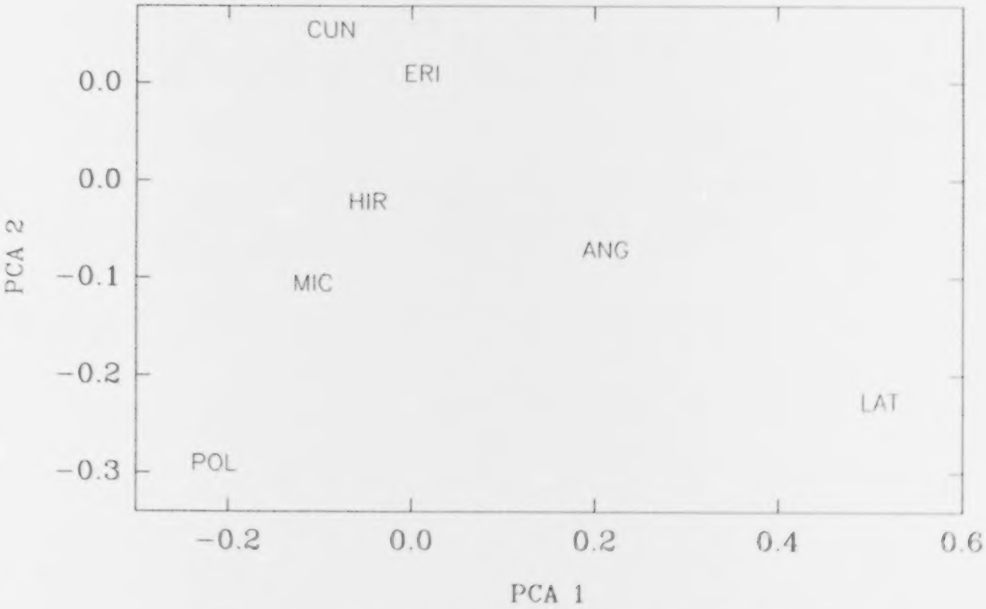


Figure 12. PCA of *Kalmia* species based on flavonoid aglycone characters (Appendix 3, II). PCA 1 accounts for 39.39%, and PCA 2 22.71% of the variation.

ANG = *K. angustifolia*; CUN = *K. cuneata*; ERI = *K. ericoides*; HIR = *K. hirsuta*; LAT = *K. latifolia*; MIC = *K. microphylla*; POL = *K. polifolia*.

To conclude, the present study supports the delimitation of seven species proposed by Ebinger (1974), i.e. *Kalmia angustifolia*, *K. cuneata*, *K. ericoides*, *K. hirsuta*, *K. latifolia*, *K. microphylla*, and *K. polifolia* (Table 1). Four varieties involving two species are recognized, 1) *Kalmia angustifolia* var. *angustifolia* and *K. angustifolia* var. *carolina* delimitated by Ebinger (1974) (Table 2); and 2) *Kalmia ericoides* var. *ericoides* and *K. ericoides* var. *aggregata* delimitated by Judd (1983) (Table 4). The proposed *K. microphylla* var. *microphylla* and *K. microphylla* var. *occidentalis* (Ebinger 1974) are not recognized.

C. Phylogenetic interpretations within *Kalmia*

Southall and Hardin (1974) succeeded to construct a cladogram of *Kalmia* species using the "Wagner Groundplan Divergence" method. In their tree (Fig. 13), *K. latifolia* was taken as the ancestor (root) to all other nine *Kalmia* species (see Table 1 for species identity). Three branches come out of the root, 1) *Kalmia angustifolia* and *K. carolina* (*K. angustifolia* var. *carolina*); 2) *K. cuneata*, *K. hirsuta* and *K. ericoides*; 3) *K. microphylla*. *Kalmia polifolia* is dangling near the *K. microphylla*. In general, they considered *K. latifolia* as the most primitive species, *K. angustifolia*, *K. cuneata*, *K. carolina*, and *K. hirsuta* are next, *K. polifolia*, *K. microphylla*, and *K. ericoides* are the most advanced. They speculated that *K. angustifolia* and *K. carolina* could have had a common ancestor, or one of them could have given rise to another. *K. polifolia* and *K. microphylla* could have had a common ancestor. *K. hirsuta* is considered to be the ancestor of *K. ericoides*.

To some extent, the present study supports Southall and Hardin's hypothesis. First, *K. latifolia* is no doubt the most primitive species by having flavonoids such as chalcones, dihydrochalcones, and aurones. It is possible that *K. latifolia* or its direct ancestor gave rise to the other *Kalmia* species. Second, *K. angustifolia* appears more similar to *K. latifolia* by sharing the three primitive flavonoid types mentioned above. The whorled leaves of *K. angustifolia* should not be overly considered because this character is inconsistent. Some *K. angustifolia* plants display both alternate leaves near the base and whorled leaves above. Also, some *K. latifolia* plants from higher elevations in the Appalachians are shorter, and have subwhorled leaves (pers. obs.). *Kalmia angustifolia*

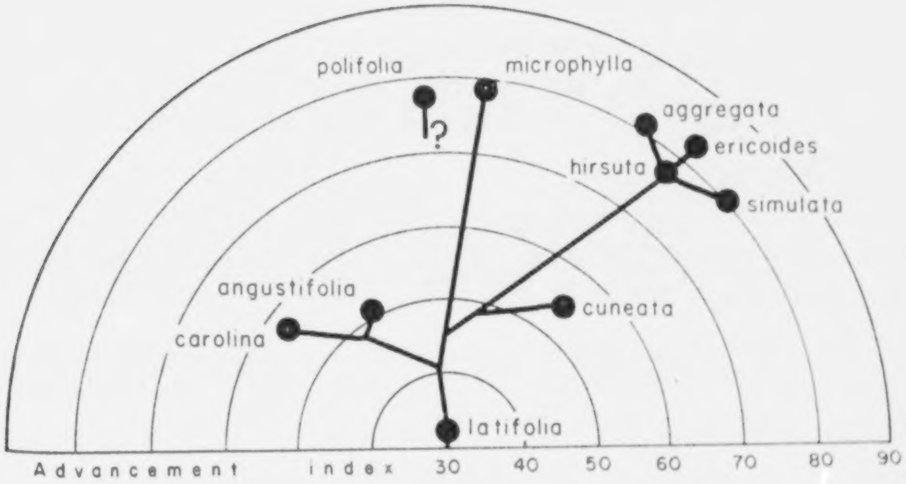

polifolia
microphylla
?
aggregata
ericoides
hirsuta
simulata
angustifolia
cuneata
carolina
latifolia
Advancement index
30
40
50
60
70
80
90

Figure 13. Proposed phylogenetic relationships within *Kalmia* (Southall and Hardin 1974).

var. *angustifolia* could have given rise to *K. angustifolia* var. *carolina*, since the latter exhibits a more diverse and advanced flavonoid profile. Third, if all other species have diverged from *K. latifolia* or its direct ancestor in a common lineage, *K. cuneata* could have split off from this lineage earlier than *K. microphylla* and *K. hirsuta*. *Kalmia hirsuta* gave rise to *K. ericoides*, which diverged further into two varieties with the var. *ericoides* on the Cuban mainland as the ancestral stock. The close relationship between *K. polifolia* and *K. microphylla* is supported by the present study.

Jaynes (1969) rejected the possibility that *K. polifolia* had an autopolyploid origin from *K. microphylla*. He also rejected that it had allotetraploid origin from *K. microphylla* and another extant *Kalmia* species. He speculated that it originated through hybridization between *K. microphylla* and a now extinct species. This study supports Jaynes' rejection of *K. microphylla* as a sole ancestor, since the flavonoid profile of *K. microphylla* does not contain two C-methylated flavones and aurone #2, both of which are principal compounds in *K. polifolia*. Considering the overall flavonoid similarity between the two species (Tables 8 and 9), it is unlikely that *K. polifolia* acquired the flavonoids independently, or that *K. microphylla* have lost them after giving rise to *K. polifolia*. If we accept Jaynes' second rejection and search for the possible extinct species that hybridized with *K. microphylla* and gave rise to the tetraploid *K. polifolia*, my judgement is that the possible candidate should be closely related to the present day *K. hirsuta*, since the flavonoid profiles of *K. microphylla* and *K. hirsuta* complement each other and make up the necessary *K. polifolia* flavonoid profile (Tables 8 and 9; Fig. 11). Furthermore, *K. hirsuta* might be able to cross with *K. microphylla*, but the right combinations are difficult to make because both are variable species. Even if we accept that the cross between *K. microphylla* and *K. hirsuta* is impossible, it does not exclude the possibility that the two could have been able to cross in the past and gave rise to *K. polifolia*. In summary, although the exact ancestors of *K. polifolia* may be difficult to determine, all the evidence from the present study points to two species, *K. microphylla* and *K. hirsuta*.

IV. Phytogeography

In this chapter a brief phytogeographical discussion of the family *Ericaceae* will be presented and followed by a similar discussion of the genus *Kalmia*. The *Ericaceae* is included because *Kalmia* has been shown to be one of the most primitive genera in the family (Judd and Kron 1993), and a better understanding of which will be beneficial to that of *Kalmia*.

The family *Ericaceae* is cosmopolitan in distribution and it appears to have emerged relatively early in angiosperm evolution, with the oldest fossils being found in the Dakota formation at Cenomanian age (late Cretaceous, ca. 95 million years ago) (Chesters *et al.* 1967). Seed fossils attributed to *Rhododendron* and *Vaccinium* have been found in Palaeocene deposits in England (Collinson and Crane 1978; Cronquist 1981). Cronquist (1981) considered that the ancestor of the *Ericaceae* originated in tropical mountains. Hutchinson (1973) regarded the South African genus *Erica* (ca.650 species) as a derived taxon originating from taxa in the Northern Hemisphere, a theory which is supported by the fact that the *Ericaceae* is absent from most of Australia, where it is largely replaced by the related family *Epacridaceae* (Heywood 1978). Pollen representing either the *Ericaceae*, *Epacridaceae*, or *Clethraceae* was reported from the Maastrichtian in the Northern Hemisphere, and only from the Eocene in Australia (Cronquist 1981).

The opposing point of view is that South African *Erica* was derived from the South American genus *Tepuia*, and then spread to Europe (Camp 1947). However, Camp was also puzzled by the fact that *Tepuia* was only found on one South American mountain. This view was restated by Maguire (1970), based on the close affinity of two South American genera, *Tepuia* and

Ledothamnus, with South African *Erica*. Stevens (1970b) analyzed another pair, an African genus *Agauria* and a South American genus *Agarista*. They are more closely related to one another than to other genera, and have similar habitat requirements. He attributed this distribution pattern to continental drift in the early part of the Cretaceous. Raven and Axelrod (1974) stated that "the common ancestor of *Gaultheria* and *Pernettya* probably arrived in southern South America by long-distance dispersal, and then spread there". Although it is hard to determine the ancestor of the *Ericaceae* and its place of origin, it is probably safe to state that the family originated somewhere outside North America.

Kalmia is endemic to North America and Cuba (Fig. 1) and five fossil species of *Kalmia* were reviewed by Ebinger (1974) who considered all of them to be dubious members of the genus as they were described from leaf impressions, using characters such as leaf size, shape, and texture, which he considered as unreliable. *Kalmia brittoniana* Hollik (1892) was found in New York, North Carolina, and Alabama and is Upper Cretaceous in age. Its leaf is described as 0.7 x 2.7 cm, with prominent midribs and no secondary veins. This is probably not a member of the genus or not even a member of *Ericaceae* (Ebinger, 1974). It was not considered as a member of *Ericaceae* in the compilation of angiosperm fossils by Chesters *et al.* (1967). *Kalmia elliptica* Brown (1962) was found in Wyoming and Colorado and is Paleocene in age. The leaf illustrated is ca. 6.8 x 16 cm (can be 1.7-6.5 x 4.2-16 cm, see Hickey, 1977), elliptic, entire margined. It was described as being closely related to the present day *Kalmia latifolia*. This fossil species was later validated (designation of the type) by Watt (1971). Ebinger (1974) regarded the species as a doubtful member of *Kalmia*. Hickey (1977) described the same species in detail from the Golden

Valley Formation (Early Tertiary), North Dakota. He considered Brown's assignment of this fossil form to *Kalmia* as the best match based on the available features. *Kalmia saxonica* Litke was found in the Lower Miocene of Germany (Litke 1968; Gothan and Weyland 1973). The description of this species was based on a fossil that consists of pieces of cuticle with the upper epidermis occasionally attached. It was considered to be very similar to *Kalmia latifolia* and it is possible that this fossil represents a member of this genus or a closely related genus of the *Ericaceae* (Ebinger 1974). *Kalmia ? elongata* Ashlee was found in the Latah formation, 3 miles west of Elk River, Idaho, and is the Upper Miocene in age (Ashlee 1932). The collection consists of two leaves which are sub-coriaceous, entire, narrowly elliptical, and a petiole 2-4 mm long. The leaves are superficially similar to *K. microphylla* (Ebinger 1974), but the fifth fossil is a representative of the extant species, *Kalmia polifolia*, and was found in British Columbia and New Hampshire, and is Pleistocene in age. The fossils were considered to be the representatives of the flora that migrated northward in the wake of the retreating Wisconsinan ice-sheet (Hollik, 1931).

Whether the above described fossils are *Kalmia* is hard to verify. Perhaps all of them, except *K. brittoniana*, are *Kalmia* or closely related plants based on the primitiveness of extant *Kalmia* and phytogeographical evidence. Morphologically, *K. latifolia* is the only species that is regarded as arborescent (Sargent 1893, 1922; Britton 1908; Little 1979; Elias 1980; Preston 1989) which itself is a relatively primitive character in angiosperms. The anatomical evidence also supports this contention (Copeland 1943). The present study also indicates that *Kalmia* is the most primitive genus in the tribe *Phyllodoceae* based the flavonoid profiles (unpubl. data). Perhaps cytology offers additional support for this view. If we accept that the base (primitive) chromosome number is x=12 in the *Ericaceae* (Raven 1975), and that x=13 is secondary (Böcher 1981), *Kalmia* which has x=12, may be one of the more primitive genera in the family. The history of the genus could be as long as that of *Rhododendron* which has x=13, and is a component of the European Arctotertiary geoflora (Collinson and Crane 1978; Mai 1989; see Mai 1991 for other flora terms commonly in use, and a comparison of those terms in space, time, and vegetation composition).

Kalmia latifolia or its immediate ancestor could have been members of the Arctotertiary geoflora of both Eurasia and North America. Southall and Hardin (1974) also speculated that *Kalmia* arose from an unknown ancestor in Tertiary times. Therefore North America may not be the place of origin of the genus and we could question the hypothesis postulated by Southall and Hardin (1974) who, using Cain's (1944) criteria for determining center of origin, suggested that *Kalmia* originated in the southern Appalachians. This contention can be substantiated as the Tertiary floras were rather evenly spread throughout the Northern Hemisphere and that there was active biotic exchange by land bridges, "stepping stones", and long distance dispersal, between North America and Eurasia during the Tertiary (Brown and Gibson 1983; Budantsev 1992; Daubenmire 1978; Friis *et al.* 1987; Graham 1972; Krutzsch 1989; Mckenna 1983; Niklas 1981; Raven and Axelrod 1974; Taylor 1990; Tiffney 1985a, 1985b; Wolfe 1985, 1987; Zhilin 1989). Even North America, especially western North America, had quite different floras in the Tertiary times. Floras similar to those of modern southeastern North America, where *K. latifolia* is distributed today, were also found in Western North America in the Tertiary (Brown and Gibson 1983; Chaney 1947; Daubenmire 1978; Leopold and MacGinitie 1972; Taylor 1990;

Wolfe 1969, 1972, 1977, 1981, 1985, 1987). The present distribution of *K. latifolia* could have resulted from two historical events: 1) the extinction of this species, or its immediate ancestor, from the Old World due to the late Tertiary cooling or due to the Quaternary glaciations; 2) the shrinking of its distribution in North America as the Rocky Mountains arose. It is well known that many plant species became extinct during the Quaternary glaciations in Europe where plant migrations were badly hindered by the west-east oriented mountain ranges (Hammen *et al.* 1971). In North America, the Cordilleran floras took on their modern aspects in late Oligocene about 27 million years ago (Axelrod and Raven 1985) or after the Oligocene (Leopold and MacGinitie 1972). The present Intermountain steppes in western North America developed during the Pliocene while grasslands in central North America developed in the late Miocene or later (Wolfe 1985). The validity of *K. latifolia* related fossils found in the Rocky Mountains may be doubted (Ebinger 1974), but at the same time it is likely that *K. latifolia* or its closely related species could have been present in western North America before those events took place in the early Tertiary. In conclusion, the place of origin of *Kalmia* may be quite different from its present geographic distribution, probably in Eurasia where the *Ericaceae* could have originated (discussed earlier). *Kalmia latifolia* is not only the most primitive member of the genus, but also of the entire tribe *Phyllodoceae*, or even the *Ericaceae* (Judd and Kron 1993), and it could have been a component of Arctotertiary floras and widely distributed in the Tertiary.

One topic related to phytogeography is dispersal, which, as far as is known, has not been explored in *Kalmia*. In *Kalmia*, vegetative reproduction using stem cuttings is possible only with the proper use of growth hormones, and a suitable growth environment (Jaynes 1988a). In nature, the long rhizomatous stems of *K. microphylla*, *K. polifolia*, *K. cuneata*, and *K. angustifolia* can generate adventitious buds, but they can only serve as a means of reproduction within limited time and space. The capsules of *Kalmia* may facilitate seed dispersal by possessing sticky glands on the capsule surface, and may be carried away by passing animals. Categorically, however, *Kalmia* are wind-dispersed since they have dry fruits (Rathcke 1988b). All seeds of *Kalmia* are small, ranging from 0.4 mm in *K. hirsuta* to 2 mm in *K. polifolia* (including the wings if present). The seeds of *K. latifolia*, *K. angustifolia*, *K. microphylla*, and *K. polifolia* have wings which range from about 0.5 mm in *K. polifolia* to ca. 0.1 mm in *K. latifolia* (Southall and Hardin 1974; Jaynes 1988a). Perhaps the long distance seed dispersal is via foraging birds or animals, which would contaminate their feet with *Kalmia* seeds in bogs or other wet habitats and carry the seeds to new areas. The wings of *Kalmia* could facilitate the wind dispersal for short distances. Most likely they may serve to enlarge the surface area in order to increase buoyancy so that the seeds stay close to the muddy surface. This may explain the fact that *K. microphylla* can be found on phytogeographic islands, such as isolated alpine meadows.

Kalmia angustifolia is probably a direct descendant of *K. latifolia* and could have diverged rather recently in eastern North America, since they share many flavonoid characters and are relatively similar morphologically. The two varieties within *K. angustifolia* could be even younger and their differentiation may well be the result of the Quaternary glaciations. The migration of plants southward during glaciations and northward at interglacial times is believed to have caused the differentiation of many plant species (Brown and Gibson 1983). *Kalmia angustifolia* var.

carolina consists of apparently disjunct populations which are declining because their natural habitats are quickly disappearing (pers. obs.).

Kalmia microphylla originated probably from *K. latifolia* or its closely related taxon in the Tertiary and the present study suggests that its ancestral populations are represented by plants from the Pacific lowland area from Washington to Alaska. The populations resemble *K. latifolia* in flavonoid profiles by sharing the aurone #1 and dihydrochalcones, and they are more robust morphologically than populations from other areas. Although the exact origin of *K. microphylla* is nearly impossible to determine, it is probably the product of the late Tertiary cooling which, combined with the elevation of the Rocky Mountains, may be also responsible for the disappearance of *K. latifolia* from western North America. *Kalmia microphylla* apparently diverged morphologically and chemically during the late Tertiary cooling, especially during the Quaternary glaciations.

Western North America comprises a rather diverse geographical area where the extent of glaciation in the Quaternary times differs from one area to another. The modern pattern of plant distributions may well reflect the extent of the last Wisconsin glaciation. The most recent syntheses of what is known about the last glaciation in North America are those of Ruddiman and Wright (1987), Fulton (1989), Wright (1989), and also Huntley and Webb (1988) from a vegetation perspective. What concerns biogeographers most is the extent of the glaciation, the exact areas covered by ice-sheet during the last glaciation. Biologists have presented evidence that appears to show the presence of ice-free refugia or corridors in western North America during the last glaciation (Ives 1974; Lynch 1988;

Matthews *et al.* 1989, and the literatures cited therein; Packer and Vitt 1974). Some of the cases have the support of geological evidence, while others are at odds with it.

Some flavonoids of *Kalmia microphylla*, clearly have a unique distribution pattern (Fig. 4). Dihydrochalcones, along with the aurone #1, are primarily found in the Queen Charlotte Islands - Vancouver - Vancouver Island - Washington lowland areas, but dihydrochalcones are also found in southwestern Northwest Territories, northern British Columbia, and the foothills of Alberta besides the area south of the southern Wisconsinan limit as proposed by Prest (1984). The above areas were either south of the ice-sheets during the last glaciation, or in the proposed ice-free refugial areas during the last glaciation. Several areas in the north Pacific coast in North America have been postulated to contain ice-free refugia, such as Vancouver Island, Queen Charlotte Islands, coastal Alaska, and Kodiak Island (Matthews *et al.* 1989; Karlstrom and Ball 1969). Northern Yukon and adjacent Northwest Territories, and the foothills of Alberta were proposed as ice-free corridors (Packer and Vitt 1974; Denford 1984; Downie and Denford 1986; Bayer 1989; Matthews *et al.* 1989). None of the above mentioned ice-free areas except Kodiak Island and northern Yukon is fully supported by geological evidence, and the newly revised map of Wisconsin glaciation ice coverage (Fulton 1989, Fig. 3, p. 7) shows that the proposed ice-free corridor at the foothills of Alberta, Vancouver Island, and Queen Charlotte Islands were all ice-covered. The present study supports the presence of these proposed ice-free areas such as Northern Yukon and adjacent North west Territories, the foothills of Alberta, Queen Charlotte Islands, and Vancouver Island. On the other hand post glaciation dispersal cannot be ruled out. If post glaciation dispersal is accepted, it is likely that *K. microphylla* may have occupied the areas on both sides of Rocky Mountains south of the ice-sheet, and in the ice-free area in northern Yukon or adjacent Northwest Territories north of ice-sheet during the last glaciation. Only if that holds true can we explain the present geographic distribution of dihydrochalcones (Fig. 4). Plants of *K. microphylla* migrated with the retreat of the ice-sheet, and in the process flavonoid profiles of certain populations changed, and most notably losing dihydrochalcones.

The Cuban species *K. ericoides* has close affinities to *K. hirsuta* of Florida. The present study supports the hypothesis that *K. hirsuta* is the ancestor of *K. ericoides* (Southall and Hardin 1974). Geologically, Cuba is Cretaceous in origin (around 125 m.y. ago) and possibly connected with North America through the modern Yucatan Peninsula, Mexico from the Late Cretaceous to the early Eocene epoch (Pindell and Dewey 1982; Guyer and Savage 1986). During the Quaternary glaciations the sea level could have dropped as far as 130 m below modern levels (the estimated range is from -60 m to -132 m) (Savin and Douglas 1985). Florida and Cuba could have been linked through the exposed Keys, and the Isle of Pines would have been joined to the Cuban mainland during the Quaternary glaciations (Brown and Gibson 1983). Therefore there are two possible ways for *K. hirsuta* to have reached Cuba: by land bridge before the separation of Cuba from the Yucatan Peninsula at the early Eocene, or by long dispersal across a narrow strait at Quaternary. The vegetation of Cuba has been shown to have a close affinity with the Yucatan vegetation (Graham 1973; Espejel 1987; Borhidi 1985), but the study carried out by Estrada-Loera (1991) clearly indicates that it is much closer to the vegetation of Florida than that of Yucatan. In the case of *Kalmia*, it is likely that *K. hirsuta* reaching Cuba by way of Yucatan Peninsula before the Early Eocene is low for two reasons: 1) *K. hirsuta* might not have existed at that time; 2) the close flavonoid relationship between the two species reduces the possibility of such long isolation of the two taxa. The hypothesis that *K. hirsuta* reached Cuba from Florida by long distance dispersal and/or through "stepping stones" when the sea level dropped considerably during the Quaternary glaciations (Borhidi 1985; Southall and Hardin 1974) is eminently reasonable. The further differentiation of *K. ericoides* into two geographically separated varieties could have been caused by the same glaciation events.

Kalmia cuneata and *K. hirsuta* both have limited distributions, and their flavonoid profiles show few signs of geographical differentiation. They probably originated from *K. latifolia* in eastern North America rather early and diverged there (Southall and Hardin 1974).

Kalmia polifolia is poorly understood, phylogenetically, as discussed in the last chapter. It seems that this tetraploid species has *K. microphylla* as one of its parents. If we accept that the other parent of *K. polifolia* is extinct (Jaynes 1969), the extinct species was probably distributed in eastern North America, the center of diversity of *Kalmia*. Current studies indicate that *K. hirsuta* appears to be, or at least is closely related to, the other putative parent (Fig. 11). Therefore the question would be: How did the present day western species, *K. microphylla* come in contact with another species in eastern North America? Since *K. hirsuta* can not be artificially hybridized with *K. microphylla* (Jaynes 1968a), both must have diverged considerably after giving rise to the tetraploid *K. polifolia*, if the results of flavonoid analyses are accepted. From a historical perspective the late Tertiary cooling and Quaternary glaciations could be responsible for bringing the western and eastern parents together. Southall and Hardin (1974) suggested that *K. hirsuta* "may have been more widespread in earlier times". Phytogeographers have been trying to understand the past geological and vegetational history, especially of the Wisconsin glaciation. It is clear that the present-day habitat, commonly alpine or high latitude bog, inhabited by *K. microphylla* could have been present in the last glaciation as a narrow belt just south of the ice-sheet, or north of the ice-sheet in northwestern North America, and the belt was a dynamic one, migrating with the ice-sheet (Delcourt *et al.* 1983; Delcourt and Delcourt 1981, 1983, 1987; Jacobson *et al.* 1987; Thompson 1988; Webb 1988; Wright 1971). Although the tundra belt was narrow, about 60-100 kilometres wide at the peak of late Wisconsin glaciation (Delcourt and Delcourt 1981), it could have been sufficient for *Kalmia* to migrate. Furthermore the boreal forest immediately behind the tundra away from the ice-sheet could also have been a habitat as long as bogs were present. *Kalmia polifolia* might well be the product in an unstable dynamic ecological belt during the Quaternary glaciations. Stebbins (1984) proposed a new "secondary contact hypothesis" to account for the origin of polyploidy. He believed that "polyploidy, accompanied by hybridization, is instrumental chiefly for rapid adaptation to new ecological conditions that become available relatively suddenly". He considered that during glaciations many secondary contacts between different populations or species were repeatedly established and broken, and some of the contacts resulted in hybridizations which could produce polyploids suited to the new conditions prevailing in regions vacated by the ice. *Kalmia polifolia* could fit this model because the species seems to only grow well in disturbed areas (pers. obs.). Field observations indicate that in a typical and stable bog most of the *K. polifolia* plants have no lateral branches even though the lateral buds appear, and they tend to live separately from each other, apparently they are very poor competitors (pers. obs.). In disturbed areas *K. polifolia* tends to grow extremely well with several stems arising from the stem base below ground and each with side branches (pers. obs.). This phenomenon has been observed on frequently cleared road sides, for example the northern part of Hwy 155, Sask., and the forest floor cleared under the power-lines such as the collection site AB-004 (near Fort McMurray, Alberta).

The difficulty with following the phytogeographic history of *Kalmia*, as well as other *Ericaceae*, is the absence of generic pollen characters with which they can be separated from each other. This may be overcome in the near future, since some palynologists have successfully used pollen grains to identify local ericaceous plants (Foss and Doyle 1988). As evidence accumulates from every field, a better understanding of the subject will be reached.

V. Taxonomy

Kalmia Linnaeus, Sp. Pl. 1: 391. 1753.

Chamaedaphne Kuntze, Rev. Gen. Pl. 2: 388. 1891, non Mitchell or Moench.

Kalmiella Small, Fl. Southeast. U.S. 886. 1903.

Lectotype species: *Kalmia latifolia* L.

Evergreen or rarely deciduous shrubs or small trees. Twigs pubescent to occasionally glabrous, terete or 2-angled; buds minute, flattened, with 2 exposed valvate to overlapping scales. Leaves simple; alternate, opposite, or in whorls of 3; blade variable in size and shape, usually coriaceous; apex obtuse, acute, or acuminate; base cuneate or obtuse; margins entire, flat or revolute; adaxial surface usually shiny; petiole 0.04-4.5 cm long; exstipulate. Inflorescence in terminal or axillary corymbiform racemes, or in terminal compound corymbs, or solitary in the axils of leaves (bracts). Flowers 5-merous, actinomorphic, with hypogynous insertion. Pedicels slender, terete, usually pubescent, subtended by a pair of bracteoles in the axil of a leaf-like bract or bractlet. Calyx synsepalous, usually green or reddish, persistent in fruit; lobes 5, longer than the tube, variously pubescent or ciliate margined. Corolla sympetalous, saucer-shaped, white to pink, red or purple, with a short cylindrical tube extending into a rotate limb that is shallowly 5-lobed and commonly 10-keeled, the limb with 10 saccate pockets in which the anthers are held under tension. Stamens 10, shorter than the corolla; filaments usually filiform, glabrous or pubescent, dorsifixed; anthers 2-celled, unappendaged, short, ovoid, opening by apical slits; pollen in tetrads, with or without viscid strands. Pistil with 5 united carpels; stigma capitate, 5-lobed;

style slender, 5-grooved, straight or bent, persistent; ovary superior, 5-locular, placentation axile, placentae massive with numerous ovules; ovule anatropous, glabrous, ridged. Fruit a subglobose to globose, 5-valved, septicidal capsule usually subtended by the persistent calyx. Seeds numerous, small and light-weight, often winged; embryo minute; germination hypogeous. A genus distributed in North America and Cuba (Fig. 1). Chromosome number N = 12, 24.

KEY TO THE SPECIES OF *KALMIA*

1. Leaves alternate or in whorls; flowers solitary or in inflorescence of a fascicle, a raceme, or a panicle. .. 2

  2. Leaves in whorls of three. .... 1. *K. angustifolia*.

  2. Leaves alternate. 3

    3. Leaves deciduous; corolla white. ..... 2. *K. cuneata*.

    3. Leaves evergreen; corolla usually pink to purple. . 4

      4. Plants less than 1 m tall; leaves usually pubescent, less than 1.5 cm long; flowers mostly solitary in the axils of the leaves. 5

        5. Leaves strongly revolute; flowers clustered toward tips of twig giving the appearance of a terminal corymbiform raceme ... 3. *K. ericoides*.

        5. Leaves flat or slightly revolute; flowers scattered along the stem in the leaf axils. .... 4. *K. hirsuta*.

      4. Plants more than 1 m tall; leaves glabrous and shiny above, more than 4 cm long; flowers in a terminal panicle. .... 5. *K. latifolia*.

1. Leaves opposite; inflorescence a terminal corymbiform raceme. 6

  6. Midrib of leaves without stalked glands; seeds less than 1.5 mm long. .... 6. *K. microphylla*.

  6. Midrib of leaves with stalked glands on both surfaces; seeds more than 1.5 mm long. .... 7. *K. polifolia*.

Treatment of Individual Taxa

The following species are arranged in an alphabetical order which is also the sequence in which their names appear in the key. The description of each species is based mainly on Ebinger (1974), Southall and Hardin (1974), and personal observations of specimens ranging from 10 to 200 sheets per species. All flavonoid vouchers were observed, and are used in the description. Presentation of synonyms for each species is based on Ebinger (1974), and the original publications.

1. ***Kalmia angustifolia*** L., Sp. Pl. 1: 391. 1753.

Chamaedaphne angustifolia (L.) Kuntze, Rev. Gen. Pl. 2: 388. 1891.

Type: Pennsylvania, LINN 560.2, lectotype, specimen on the right.

An evergreen shrub to 1.5 m tall, upright, sparsely branched. Twigs terete, reddish-brown, puberulent to glabrous. Leaves in whorls of 3, rarely alternate or opposite; blade oblong to elliptic-lanceolate, 1.5-8 cm long, 0.5-2.5 cm wide, slightly coriaceous; apex obtuse to acute, usually apiculate; base obtuse to cuneate; margins usually flat; adaxial surface lightly puberulent with white short trichomes, sometimes glabrate with age, midrib puberulent; abaxial surface glabrous to puberulent, sometimes stipitate-glandular; petioles 0.6-1.6 cm long, usually puberulent. Inflorescence a corymbiform raceme, occurring in leaf axils near terminal ends of stems of previous year's growth; central axis of inflorescence less than 1.5 cm long. Pedicels 0.5-2 cm long, puberulent and sometimes stipitate-glandular, subtended by pair of bracteoles 4-5.5 mm long, in axil of lanceolate bractlet, 1-6 mm long. Calyx puberulent outside, glabrous within, usually green, sometimes the tip reddish, or reddish throughout, 3-6 mm in diameter; lobes ovate, usually acuminate, 2-2.8 mm long. Corolla reddish-purple to pink, rarely white, usually deeper coloured near the anther pockets and with a ring of red to purple spots just below the pockets, 6-13 mm in diameter, 7.5-9.5 mm long. Filaments puberulent on the lower half, 2.5-3.5 mm long; anthers purplish-brown, 0.5-1 mm long. Style 3.5-4.5 mm long. Fruit depressed globose, 3-5 mm broad, 2-3.5 mm long, puberulent and stipitate-glandular. Seeds winged, obovate, 0.6-1 mm long. Chromosome number N = 12.

Distribution and Habitat: This species is distributed in eastern North America, from Ontario, Quebec, and Newfoundland in the north, southward on the east coast to South Carolina (Fig. 14). It is fairly common in open bogs and wet areas.

Discussion: It has been shown that this species is closely related to *K. latifolia* in many respects (Jaynes 1968a, 1988; Ebinger 1974; Southall and Hardin 1974; the present study). This taxon has been treated either as two distinct species or as two varieties of the same species (see discussion in Chapter 1 and Table 2). The current study demonstrates that the two entities are separable by their flavonoid profiles (Figs. 5 and 9, Appendix 5, A), but based on structural features, they might be better treated as two varieties (already discussed in Chapter 3). This also conforms to the majority of treatments of the taxon (Table 2).

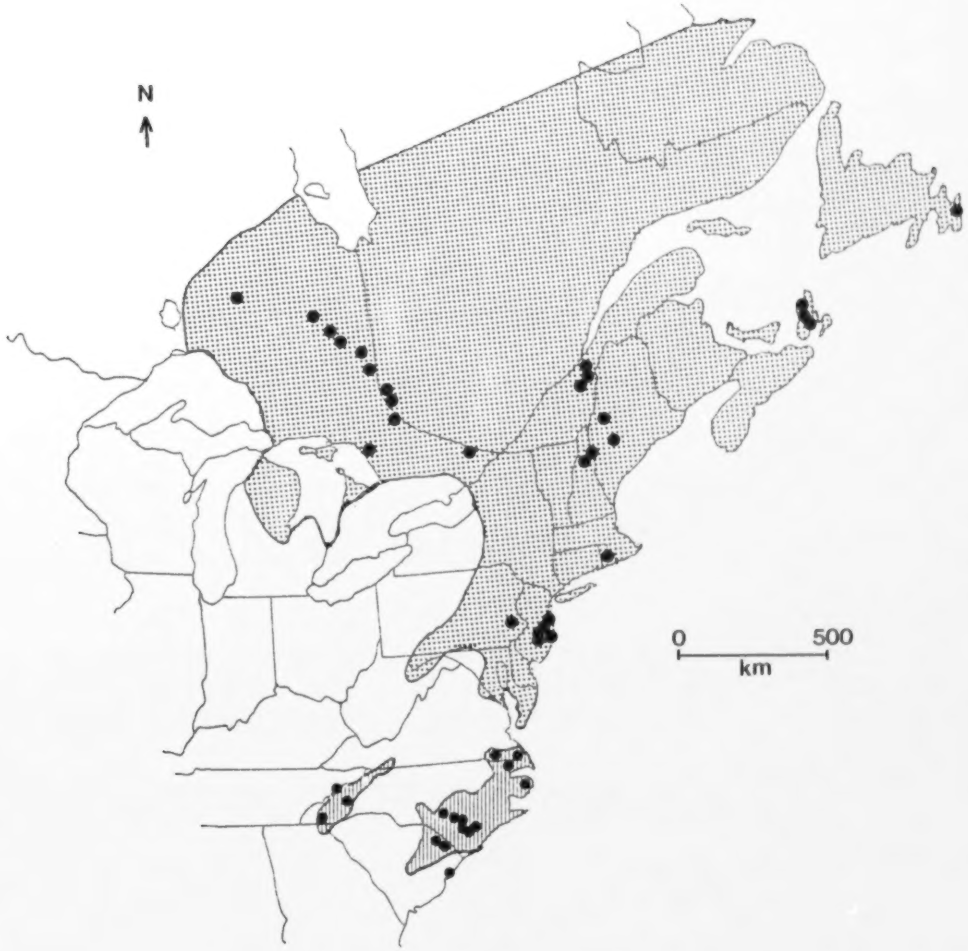


Figure 14. Distribution of *Kalmia angustifolia* var. *angustifolia* (dotted area), and var. *carolina* (vertical shading) in eastern North America. (Modified from Ebinger 1988a). Collections used in the flavonoid analyses are indicated by filled circles.

KEY TO VARIETIES

1. Calyx with dense stipitate-glands; mature leaves glabrous. .... 1a. var. *angustifolia*.

1. Calyx without stipitate-glands, or nearly so; mature leaves densely puberulent beneath. . 1b. var. *carolina*.

1a. ***Kalmia angustifolia*** L. var. ***angustifolia***.

Kalmia angustifolia β carnea Ait. Hort. Rev. 2: 64. 1789.

Kalmia angustifolia α rubra Ait. Hort. Rev. 2: 64. 1789. *Kalmia angustifolia* var. *rubra* (Ait.) Loddiges, Bot. Cab. 6: 502. 1821. *Kalmia rubra* (Loddiges) Bosse, Vollst. Handb. Blumengart. 2: 347.1841. (as synonym). *Kalmia angustifolia* f. *rubra* Voss, Blumengart. 1: 591. 1894. (without basionym). Type: unknown.

Kalmia angustifolia β oleifolia Pers. Syn. Pl. 1: 477. 1805. *Kalmia oleifolia* (Pers.) Hoffmgg., Verz. Pflanzenkulturen 70. 1824. *Kalmia angustifolia* var. *oleifolia* (Pers.) Jäger, Ziergehölze 278. 1865. (nom. nud.). Type: unknown.

Kalmia angustifolia β ovata Pursh, Fl. Amer. Sept. 296. 1814. *Kalmia angustifolia* f. *ovata* Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. (without basionym). Type: unknown.

Kalmia angustifolia var. *pumila* Forbes, Hort. Woburn. 93. 1833. *Kalmia pumila* Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. (as synonym). Type: unknown.

Kalmia angustifolia var. *rosea* Forbes, Hort. Woburn. 93. 1833. Type: unknown. *Kalmia angustifolia* f. *rosea* Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. (without basionym). Type: unknown.

Kalmia angustifolia var. *variegata* Forbes, Hort. Woburn. 93. 1833. Type: unknown.

Kalmia elliptica Raf. Autikon Bot. 87. 1840. (as synonym).

Kalmia ferruginea Raf. Autikon Bot. 86. 1840. Type: unknown.

Kalmia angustifolia var. *minima* Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. Type: unknown.

Kalmia angustifolia var. *nana* Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. *Kalmia angustifolia* f. *nana* Voss, Blumengart. 1: 591. 1894. (as synonym). Type: unknown.

Kalmia angustifolia var. *serotina* Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. *Kalmia serotina* Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. (as synonym). Type: unknown.

Kalmia pumila rubra Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. (as synonym).

Kalmia pumila serotina Bosse, Vollst. Handb. Blumengart. 2: 347. 1841. (as synonym). *Kalmia angustifolia* f. *pumila* Voss, Blumengart. 1: 591. 1894. (without basionym). Type: unknown.

Kalmia angustifolia var. *fol. varieg.* Jäger, Ziergehölze 278. 1865. Type: unknown.

Kalmia angustifolia var. *hirsuta* Jäger, Ziergehölze 278. 1865. *Kalmia angustifolia* f. *hirsuta* Voss, Blumengart. 1: 591. 1894. (without basionym). Type: unknown.

Kalmia media K. Koch, Dendrologie 2(1): 153. 1872. (as synonym). *Kalmia angustifolia* f. *media* Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. (without basionym). Type: unknown.

Kalmia intermedia Lange Ind. Sem. Hort. Hauniensi a. 1873 Collectorum: Nom. emendata 3. 1874. *Kalmia glauca β intermedia* Lange Ind. Sem. Hort. Hauniensi a. 1873 Collectorum: Nom. emendata 3. 1874. (as synonym). Type: Botanical Museum of Copenhagen (C).

Kalmia angustifolia var. *lucida* Lavallée, Arbor. Segrez. 159. 1877. (nom. nud.). *Kalmia angustifolia* f. *lucida* Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. (without basionym). Type: unknown.

Kalmia angustifolia f. *procumbens* Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. (nom. nud.). Type: unknown.

Kalmia angustifolia f. *candida* Fern. Rhodora 15: 151. 1913. *Kalmia angustifolia* var. *candida* (Fern.) Rehd. *In* Bailey Stand. Cyclop. Hort. 3: 1734. 1915. Type: Newfoundland, *Fernald & Wiegand*, no. 6019 (GH).

Mature leaves bright green above, pale glabrous or with scattered stalked glandular trichomes beneath, commonly not puberulent. Calyx puberulent and strongly stipitate-glandular. Corolla glabrous or slightly puberulent on the outside.

Distribution and Habitat: This variety is distributed from Ontario to Newfoundland, south to Virginia, in open bogs, swamps, and wet areas (Fig. 14). Duppstadt (1980) reported the discovery of *K. angustifolia* L. from Tucker County, West Virginia, which appears to be the variety *angustifolia*. Flowering is in May through July.

Common Names: Sheep Laurel, Lambkill, Sheepkill, Wicky, Narrow-leaved Kalmia, Dwarf Laurel, Pig Laurel.

Discussion: The extensive list of synonyms indicates that the variety is variable in flower colour, leaf colour and shape, and size and habit of the plant. Although such variations have been recognized at various taxonomic levels (from species to form), they essentially represent natural variation within populations and are better treated as cultivars (see Ebinger 1974; Jaynes 1988, for detailed discussions).

1b. ***Kalmia angustifolia*** L. var. ***carolina*** (Small) Fern. Rhodora 39: 437. 1937.

Kalmia carolina Small, Fl. Southeast. U.S. 886. 1903. *Kalmia caroliniana* Small, Fl. Southeast. U.S. 1336. 1903. Orthog. err. pro syn. *K. carolina*. *Kalmia angustifolia* L. var. *caroliniana* (Small) Fern. Rhodora 39: 476, 498. 1937.

Type: North Carolina: Flat Rock, June 12-16, 1858, *L.R. Gibbes* (Holotype: NY, No. 9965!).

Mature leaves commonly deep green above, pale and permanent puberulent beneath, with scattered stalked glandular trichomes. Calyx strongly puberulent usually without stalked glandular trichomes. Corolla usually densely puberulent on the outside.

Distribution and Habitat: The variety is found in open woods, shrubby bogs, pocosins, and savannas distributed in two disjunct areas (Fig. 14). One is from extreme southern Virginia along the Coastal Plain south to South Carolina. Another is in the Appalachian Mountains from Carol County Virginia to eastern Tennessee and northeastern Georgia. Flowering is in April into May.

Common Names: Sheep Laurel, Lambkill, Carolina Wicky, Carolina Bog Myrtle.

Discussion: The variety is geographically isolated from *Kalmia angustifolia* var. *angustifolia* and readily separated by the key characters.

2. ***Kalmia cuneata*** Michaux. Fl. Bor.-Amer. 1: 257. 1803.

Chamaedaphne cuneata (Michx.) O. Kuntze, Rev. Gen. Pl. 2: 388. 1891.

Type: Carolina. (Holotype: unknown; Isotype: GH).

A deciduous shrub to 1.5 m tall, upright, sparsely branched. Twigs terete, reddish-brown, slender, puberulent, sparsely stipitate-glandular, becoming glabrous and light gray. Leaves alternate; blades oblanceolate to elliptic-lanceolate, 2-6 cm long, 0.5-3 cm wide; apex obtuse to acute, apeculate; base narrowly cuneate; margin flat or slightly revolute; adaxial surface glabrous or sparsely stipitate-glandular, midrib usually puberulent; abaxial

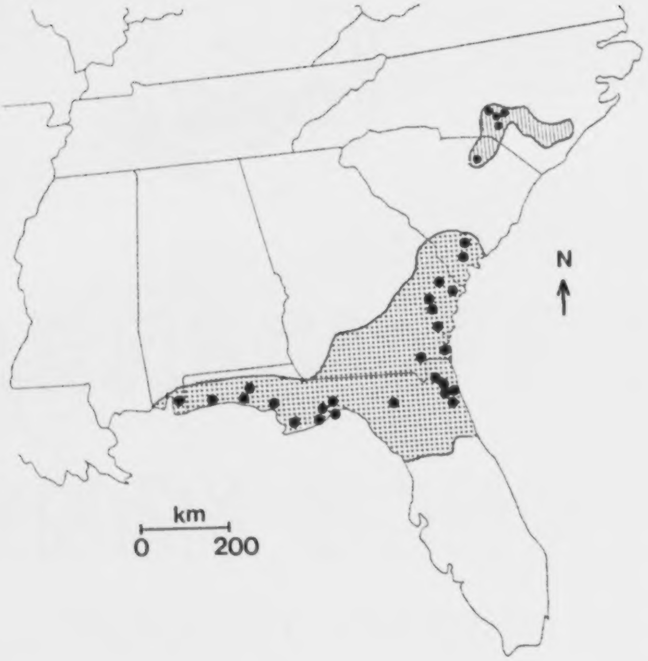


Figure 15. Distribution of *Kalmia cuneata* (vertical shading), and *K. hirsuta* (dotted area) in southeastern United States. (After Ebinger 1988a). Collections used in the flavonoid analyses are indicated by filled circles.

surface stipitate-glandular; petiole 2-4 mm long, stipitate-glandular. Inflorescence a reduced corymbiform raceme or fascicle of 3-10 flowers in upper axils of the previous year's growth; central axis of the inflorescence minute, to 3mm long. Pedicel 1.5-3 cm long, glabrous to lightly stipitate-glandular, recurved in fruit, subtended by a pair of bracteoles in the axil of a small lanceolate bractlet, 1-3 mm long. Calyx glabrous to lightly stipitate-glandular, usually green, 6-8 mm in diameter; lobes oblong, apex acute, 3-4 mm long. Corolla creamy white with a red band within, lightly stipitate-glandular outside, puberulent near the base within, 1.3-2 cm in diameter, 1.2-1.4 cm long. Filaments puberulent toward the base, 2.7-3.9 mm long; anthers purplish-brown, 1-1.3 mm long. Style 7-11.5 mm long; ovary stipitate-glandular. Fruit depressed globose, 4-6 mm broad, 2.5-3.5 mm long, puberulent and stipitate-glandular. Seeds wingless, light brown, oblong, 0.5-0.8 mm long, slightly curved. Chromosome number N = 12.

Distribution and Habitat: Wet sandy peats, shrub bogs, savannas, and sand hills in the inner Coastal Plain, North Carolina and South Carolina (Fig. 15). Flowering is in late May into June.

Common Name: White Wicky.

Discussion: The holotype of this species has not been located (Ebinger 1974) and the only known type is an isotype at the Gray Herbarium (Ebinger 1974; Southall and Hardin 1974). This species is quite distinct in the genus as it is deciduous and has white corolla. It is reported as a rare shrub, and an endangered species (Woods 1961; Southall and Hardin 1974; Southall and Nelson 1978). Kral (1983) reported that *K. cuneata* does not compete well with other bog shrubs, but "its main enemies up till now have been management schemes which involve mechanical clearing of the shrub layer, this usually accompanied by digging of drainage ditches, discing and ploughing". The reported distribution of this species in South Carolina is probably entirely based on one collection by B.E. Smith, at Hartsville, South Carolina. The label on the specimen collected by B.E. Smith reads, "Bay near Golf Course, Hartsville, S.C." (NY). Dr. Steven R. Hill at Clemson University, South Carolina points out that the plants collected at the Golf Course were probably introduced from North Carolina (personal communication, 1991). I searched for the species in and around Hartsville without any success.

The present study supports the hypothesis that the species is closely related to *K. hirsuta* (Jaynes 1968a; Ebinger 1974).

3. ***Kalmia ericoides*** Wright ex Griseb. Cat. Pl. Cub. 51. 1866.

Chamaedaphne ericoides (Wright ex Griseb.) O. Kuntze, Rev. Gen. Pl. 2: 388. 1891.

Type: Cuba, Piñar del Rio: Guane, near La Grifa, 1860-1864, *C. Wright* 2199 (Holotype: GOET; Isotypes: GH, MO, US, NY: 3 sheets, No.9967-9969!).

An evergreen, erect to spreading, sparsely branched shrub to 1 (-1.4) m tall with a thickened or burl-like basal stem. Twigs terete, light gray to reddish, slender to stout, puberulent or hispid to glabrous, with or without stipitate-glandular trichomes. Leaves alternate, sparsely or densely distributed along stem; blades linear to ovate, 3.5-14 mm long, 0.5-3 mm wide, coriaceous; apex acute, base cuneate to obtuse; margins strongly revolute; adaxial and abaxial surfaces usually lightly hispid and stipitate-glandular, sometimes strongly puberulent, rarely glabrous; petiole nearly lacking to 1.5 mm long, puberulent. Flowers solitary (or occasionally in fascicle or in compact racemes), in the axils of the leaves at the end of the branches, forming a seemingly terminal cluster; Pedicels 4-14 mm long, usually puberulent, hispid, and stipitate-glandular, subtended by a pair of bracteoles, ovate-triangular to triangular, 1-3 mm long, puberulent and stipitate-glandular with ciliated margins. Calyx usually green; lobes lanceolate, apex acute, 3-6 mm long, commonly puberulent, hispid, and stipitate-glandular, tardily deciduous in fruit. Corolla light pink to white, usually lightly hirsute and stipitate-glandular on the keels outside, slightly puberulent at the base within, 8-17 mm in diameter, 6-12 mm long. Filaments puberulent toward the base, 3-5 mm long; anthers purplish-brown, 0.7-1.2 mm long. Style 4-7 mm long; ovary usually stipitate-glandular. Fruit subglobose to ovoid, 2-4 mm broad, 1.7-3 mm long, lightly puberulent and stipitate-glandular. Seeds wingless, brown, ovoid, 0.4-0.7 mm long.

Distribution and Habitat: Sand savannas and pine barrens in western Cuba (Fig. 16). Flowering is from November through May (June).

Discussion: This species is the only *Kalmia* species outside North America. The present study strongly supports the hypothesis that the species is closely related to *K. hirsuta* (Ebinger 1974; Southall and Hardin 1974; Fig. 9, and Appendix 5, B). *Kalmia ericoides* has been studied by several investigators in recent years (Ebinger 1974; Southall and Hardin 1974; Judd 1983; Berazain and Sorribes 1987). It was recognized as a single species by everyone except Southall and Hardin (1974, Table 4). It is apparently a very variable species judging from the diverse treatments it has received. The result of the flavonoid analysis (Fig. 6) agrees with

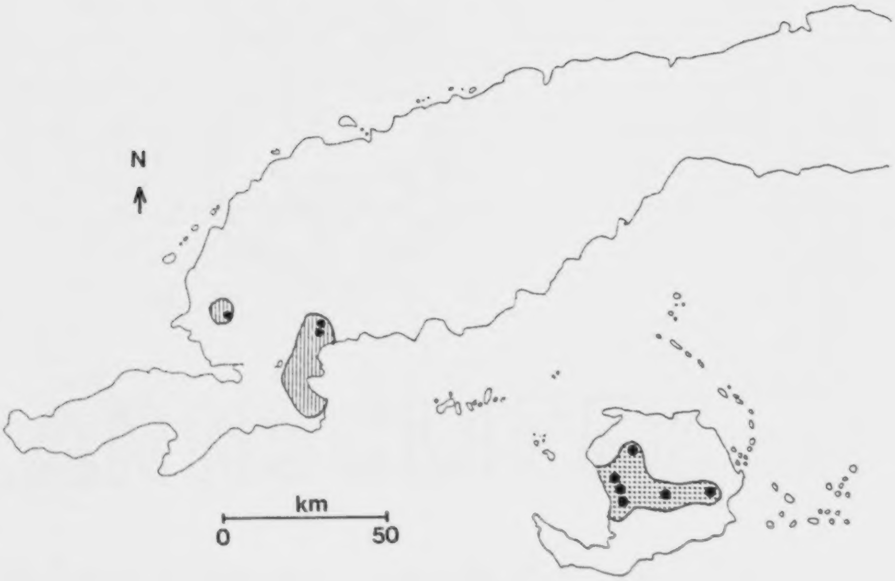


Figure 16. Distribution of *Kalmia ericoides* var. *aggregata* (dotted area) on the Isle of Pines, Cuba, and var. *ericoides* (vertical shading) on the main Island of Cuba. (Modified from Judd 1983, and Berazain and Sorribes 1987). Collections used in the flavonoid analyses are indicated by filled circles.

Judd's (1983) delimitation of two geographically separated varieties which will be followed in this study. I have to admit that the separation of the two varieties using concise key morphological characters is quite challenging. Judd (1983) has shown that key characters such as compactness of the inflorescence (Small 1914; Roig and Acuña 1957; Southall and Hardin 1974), length of the calyx lobes (Southall and Hardin 1974) are not effective in discriminating between the two varieties. It appears that all the taxonomists listed in Table 4 have tried to use pubescence as a key character. There are three major pubescence types in *K. ericoides*, unicellular (puberulent) trichome, multicellular (hispid) trichome, and multicellular glandular-headed (stipitate-glandular) trichome, both long and short (see Judd 1983 Fig. 1, p. 50). The first two kinds of trichomes, especially hispid trichomes, are common on the stems and leaves of *K. hirsuta*. Both Ebinger (1974) and Judd (1983) relied solely on pubescent characters to separate the two varieties (note they differ in delimitation, Table 4). The former uses a combination of three kinds of trichome, and the latter uses only puberulent trichome. By close examination of herbarium specimens, it seems that no single form of pubescence serves to separate the two varieties well and a combination of three kinds of trichomes should be used. It seems that the major stem and leaf pubescence for the Cuban main island var. *ericoides* is hispid, and that the Isle of Pine var. *aggregata* has mainly pubescence of both puberulent and stipitate-glandular forms. This coincides with the result of flavonoid analysis which indicates that var. *ericoides* as the direct descendant of *K. hirsuta* (Chapter 3). Variety *aggregata* appears to be derived from var. *ericoides*, with the hispid trichome being replaced by puberulent and stipitate-glandular trichomes through evolutionary time.

KEY TO VARIETIES

1. Stem, leaf adaxial surface, and pedicel hispid, lacking to sparsely covered with puberulent and stipitate-glandular trichomes. .... 3a. var. *ericoides*.

1. Stem, leaf adaxial surface, and pedicel lacking to sparsely covered with hispid trichomes, usually densely puberulent, sparsely to densely stipitate-glandular. ... . 3b. var. *aggregata*.

3a. ***Kalmia ericoides*** Wright ex Griseb. var. ***ericoides***

Kalmiella ericoides (Wright ex Griseb.) Small, North Amer. Fl. 29: 54. 1914.

Leaves usually scattered, 5-12 leaves/cm; blades 4-9 mm long, 0.5-1.7 mm wide; adaxial surface nearly glabrous to hispid, sparsely stipitate-glandular, usually not puberulent; pedicels usually longer than the subtending leaves (bracts), giving the inflorescence an open appearance. Calyx lobes 3-5 mm long, hispid and lightly puberulent on the abaxial surface, adaxial surface usually glabrous.

Common Names: not known.

Distribution and Habitat: Open white-sand savannas and pine barrens in the Province of Piñar del Rio, Cuba (Fig. 16).

3b. ***Kalmia ericoides*** Wright ex Griseb. var. ***aggregata*** (Small) Ebinger, Rhodora 76: 389. 1974.

Kalmiella aggregata Small, North Amer. Fl. 29: 54. 1914. *Kalmia aggregata* (Small) Copeland, Amer. Midl. Nat. 30: 571. 1943.

Type: Cuba, Isle of Pines: Los Indios, 17 May 1910, *Jennings* 324 (Holotype: NY; Isotype: MO).

Kalmiella simulata Britton & Wilson, Mem. Torrey Bot. Club 16: 93. 1920. *Kalmia simulata* (Britton & Wilson) Southall, Jour. Elisha Mitchell Sci. Soc. 90: 22. 1974. Type: Cuba, Isle of Pines, vicinity of Los Indios, 13 Feb. 1916, *Britton, Britton & Wilson* 14205 (Holotype: NY).

Leaves usually crowded, 15-25 leaves/cm; blades 3.5-14 mm long, 0.5-3 mm wide; adaxial surface sparsely to densely puberulent and stipitate-glandular, usually lacking hispid trichomes; pedicels usually as long as the subtending leaves (bracts), giving the inflorescence a compact to open appearance. Calyx lobes 3-6 mm long, sparsely hispid and densely puberulent on the abaxial surface, usually densely puberulent on the adaxial surface.

Common Names: not known.

Distribution and Habitat: Open white-sand savannas and pine barrens on the Isle of Pines, Cuba (Fig. 16).

4. ***Kalmia hirsuta*** Walt. Fl. Carol. 138. 1788.

Chamaedaphne hirsuta (Walt.) O. Kuntze, Rev. Gen. Pl. 2: 388. 1891. *Kalmiella hirsuta* (Walt.) Small, Fl. Southeast. U.S. 886. 1903.

Type: South Carolina (BM).

Kalmia ciliata Bartr., Trav. v, 7, 18, 94, 171, 242. 1791; ed. 2, iv, 7, 92, 169, 240. 1792. Type: unknown.

An evergreen spreading to ascending, sparsely branched shrub to 0.6 (-1.2) m tall with a thickened or burl-like basal stem. Twigs terete, slender, reddish brown, becoming gray, puberulent and densely hispid. Leaves alternate; blades elliptic to ovate, 5-14 mm long, 1.5-8 mm wide, coriaceous; apex acute, ending in a rounded point, white to orange; base cuneate to obtuse; margins slightly revolute; adaxial and abaxial surfaces usually puberulent and hispid, with stipitate-glandular trichomes, rarely glabrous; petiole nearly lacking to 1 mm long. Flowers solitary (or occasionally in a fascicle of 2-5 or in compact racemes), in the axils of the leaves (bracts) at present year's growth. Pedicels 3-20 mm long, hispid, and stipitate-glandular, subtended by a pair of bracteoles, 4-6 mm long, usually puberulent, hispid, and stipitate-glandular. Calyx green; lobes foliaceous, lanceolate, apex acute, 3-8 mm long, puberulent, hispid, and stipitate-glandular, tardily deciduous in fruit. Corolla pink (rarely white), marked with red near the anther pockets and with a ring of red spots lower down, usually lightly hirsute and stipitate-glandular on the keels outside, puberulent at the base within, 10-15 mm in diameter, 8-10 mm long. Filaments puberulent toward the base, 3-4 mm long; anthers purplish-brown, 0.7-1.3 mm long. Style 5-7.5 mm long; ovary usually stipitate-glandular. Fruit subglobose to ovoid, 2-4 mm broad, 2-3.5 mm long, lightly stipitate-glandular. Seeds wingless, light brown, ovoid, 0.25-0.5 mm long. Chromosome number N = 12.

Distribution and Habitat: Open sandy savannas, sand hills, and pine barrens on coastal plains of southern Alabama, northern Florida, Georgia, and the southeastern corner of South Carolina (Fig. 15). Flowering is from May through July.

Common Names: Sandhill Laurel, Calico-bush, Hairy Kalmia.

Discussion: *Kalmia hirsuta* is closely related to *K. ericoides*. The species has a relatively limited distribution and shows little morphological variation among populations (Southall and Hardin 1974). One of the key characters of *K. hirsuta* is the presence of hispid trichomes on the plant parts, but occasionally plant is completely glabrous, with leaves superficially like *K. microphylla* or *K. polifolia*.

5. ***Kalmia latifolia*** L., Sp. Pl. 1: 391. 1753.

Chamaedaphne latifolia (L.) O. Kuntze, Rev. Gen. Pl. 2: 388. 1891.

Type: LINN 560.1, lectotype, specimen at the top right.

Kalmia latifolia var. *acuminata* Raf. Medical Fl. 2: 17. 1830. (nom. nud.).

Kalmia latifolia var. *alba* Raf. Medical Fl. 2: 17. 1830. = *Kalmia latifolia* f. *alba* (Mouillefert) Rehd.

Kalmia latifolia var. *arborea* Raf. Medical Fl. 2: 17. 1830. (nom. nud.).

Kalmia latifolia var. *maculata* Raf. Medical Fl. 2: 17. 1830. Type: unknown. = *Kalmia latifolia* f. *fuscata* (Rehd.) Rehd.

Kalmia latifolia var. *ovatifolia* Raf. Medical Fl. 2: 17. 1830. (nom. nud.). = *Kalmia latifolia* f. *obtusata* (Rehd.) Rehd.

Kalmia latifolia var. *ternata* Raf. Medical Fl. 2: 17. 1830.

Kalmia latifolia β salicifolia Forbes, Hort. Woburn. 93. 1833. Type: unknown. = *Kalmia latifolia* f. *angustata* Rehd.

Kalmia nitida Forbes, Hort. Woburn. 93. 1833. Type: unknown.

Kalmia latifolia var. *myrtifolia* Bosse, Vollst. Handb. Blumengart. 2: 348. 1841. *Kalmia latifolia* f. *myrtifolia* (Bosse) K. Koch, Dendrologie 2(1): 153. 1872. *Kalmia myrtifolia* Andre, Revue Hort. 55: 10. 1883. Type: unknown.

Kalmia latifolia var. *coronata* Gray, Amer. Nat. 2: 324. 1868. Type: Massachusetts: woods near Framingham, *James*

Parker (GH). = *Kalmia latifolia* f. *fuscata* (Rehd.) Rehd.

Kalmia latifolia f. *minor* K. Koch, Dendrologie 2(1): 153. 1872. Type: unknown. = *Kalmia latifolia* f. *myrtifolia* (Bosse) K. Koch.

Kalmia latifolia f. *rubra* K. Koch, Dendrologie (2) 1: 152. 1872. *Kalmia latifolia* var *rubra* (K. Koch) Rehd. *In* Bailey, Cyclop. Amer. Hort. 2: 854. 1900. Type: unknown.

Kalmia lucida K. Koch, Dendrologie (2) 1: 152. 1872. (as synonym).

Kalmia latifolia var. *minor* Lavallée, Arbor. Segrez. 159. 1877. (as synonym of *K. latifolia* var. *nana*).

Kalmia latifolia var. *nana* Lavallée, Arbor. Segrez. 159. 1877. (nom. nud.); Mouillefert, Traité Arb. Arbrisse 2: 1027. 1897. Type: unknown. = *Kalmia latifolia* f. *myrtifolia* (Bosse) K. Koch.

Kalmia latifolia var. *parvarti* André, Revue Hort. 60: 541. 1888. Type: unknown.

Kalmia latifolia var. *polypetala* Nicholson, Hand-list Trees Shrubs Arb. 2: 49. 1896. *Kalmia latifolia* f. *polypetala* (Nicholson) Beissner, Schelle, & Zabel, Handb. Laubholz-Benennung. 386. 1903. *Kalmia latifolia* f. *polypetala* (Nicholson) Rehd. Rhodora 12: 1. 1910. Type: Massachusetts: near South Deerfield, *Miss M. Bryant* (GH).

Kalmia latifolia alba Mouillefert, Traité Arb. Arbrisse 2: 1027. 1897. *Kalmia latifolia* f. *alba* (Mouillefert) Rehd. Rhodora 12: 2. 1910. Type: unknown.

Kalmia latifolia monstruosa Mouillefert, Traité Arb. Arbrisse 2: 1027. 1897. Type: unknown. = *Kalmia latifolia* f. *polypetala* (Nicholson) Beissner.

Kalmia latifolia var. *fuscata* Rehd. Möller's Deutsch. Gart. Zeit. 18: 578. 1903. *Kalmia latifolia* f. *fuscata* (Rehd.) Rehd. Rhodora 12: 2. 1910. Type: New York: Canaan Four Corners, *Dr. Childs* (GH).

Kalmia latifolia var. *obtusata* Rehd. Möller's Deutsch. Gart. Zeit. 18: 577. 1903. *Kalmia latifolia* f. *obtusata* (Rehd.) Rehd. Rhodora 12: 2. 1910. Type: Connecticut: near Pomfret, *Bowditch*.

Kalmia latifolia var. *laevipes* Fern. Rhodora 42: 53. 1940. Type: Virginia: Norfork Co.: dry woods of a "hammock", Great Dismal Swamp, west of Yadkin, *Fernald* & *Long* 11,101 (Holotype: GH; Isotype: Herb. Phil. Acad.).

Kalmia latifolia f. *angustata* Rehd. Jour. Arnold Arb. 26: 481. 1945. Type: New Jersey: Cape May Co.: Dennis township, *H.A. Scribner* (GH).

An evergreen shrub or rarely a small tree to 8 (-12) m tall. Twigs terete, reddish-brown, becoming gray, viscid stipitate-glandular, glabrate with age. Leaves alternate or seemingly whorled on slow growing twigs; blade flat, elliptic to elliptic-lanceolate, 4-12 cm long, 1.5-5 cm wide, coriaceous; apex acute; base cuneate; adaxial surface dark green, glabrous, with midrib puberulent; abaxial surface light green to light brown, stipitate-glandular, glabrate with age; petioles 1-3 cm long, glabrous to puberulent, sometimes stipitate-glandular. Inflorescence a terminal, compound corymb (panicle); major inflorescence branches to 5 cm long; puberulent, stipitate-glandular. Pedicels 1.5-4 cm long, puberulent to stipitate-glandular, often floccose, viscid, rarely glabrous, subtended by a pair of bracteoles in the axil of a puberulent lanceolate bractlet, 1-5 mm long. Calyx glabrous to stipitate-glandular, green to reddish, 5-8 mm in diameter; lobes usually oblong, acute, 3-3.5 mm long. Corolla usually pink (ranging from deep red to white) with purple spots around each anther pocket, usually lightly stipitate-glandular outside, puberulent inside, 1.5-3 cm in diameter, 2-2.5 cm long. Filaments puberulent, 4-5 mm long; anthers dark purple to brown, 1.2-1.7 mm long. Style 1-1.8 cm long. Fruit depressed globose, stipitate-glandular, 4-7 mm broad, 3-5 mm long. Seeds winged, obovate and curved, 0.5-1 mm long. Chromosome number N = 12.

Distribution and Habitat: The species is found in rocky or sandy hardwood forests on mountain slopes, ravines, or in pure dense thickets at higher elevations in eastern North America, from southern Maine in the north, west to Ohio, south to northwestern Florida, Alabama, and Mississippi (Fig. 17). Flowering is from April to June.

Common Names: Mountain Laurel, Broad-leaved Laurel, Calico-bush, Spoonwood, Ivy, Mountain Ivy, Big-leaved Ivy, Laurel-leaves, Calmoun, American Laurel.

Discussion: The tallest *K. latifolia* I observed was about 8 m tall at Cliffside Lake, near Highlands, North Carolina. Southall and Hardin (1974) reported that the plant can reach 12 m high. *Kalmia latifolia* has been shown to be the most primitive member of the genus (Southall and Hardin 1974; present study). Although showing considerable morphological variation (Ebinger 1974; Southall and Hardin 1974), its flavonoid profiles show little variation among populations (Fig. 9). Therefore a single species is recognized, for forms and cultivars of *K. latifolia*, one can refer to Ebinger (1974) and Jaynes (1988a, 1988b). Mountain Laurel is a very showy and beautiful American indigenous plant, Sprague (1871) once said that "no words can describe the beauty of this plant on the mountains of the Middle States, where it covers acres, and sheets whole hillsides with pink and white".

6. ***Kalmia microphylla*** (Hook.) Heller, Bull. Torrey Bot. Club 25: 581. 1898.

Kalmia glauca Ait. γ *microphylla* Hook. Fl. Bor.-Amer. 2: 41. 1834. *Kalmia polifolia* var. *microphylla* Rehd. *In* Bailey, Cyclop. Am. Hort. 2: 854. 1900. (without basionym); (Hook.) Rehd. *In* Bailey, Stand. Cyclop. Hort. 3: 1734. 1915. *Kalmia polifolia* var. *microphylla* (Hook.) Hall, Univ. California Publ. Bot. 4: 201. 1912.

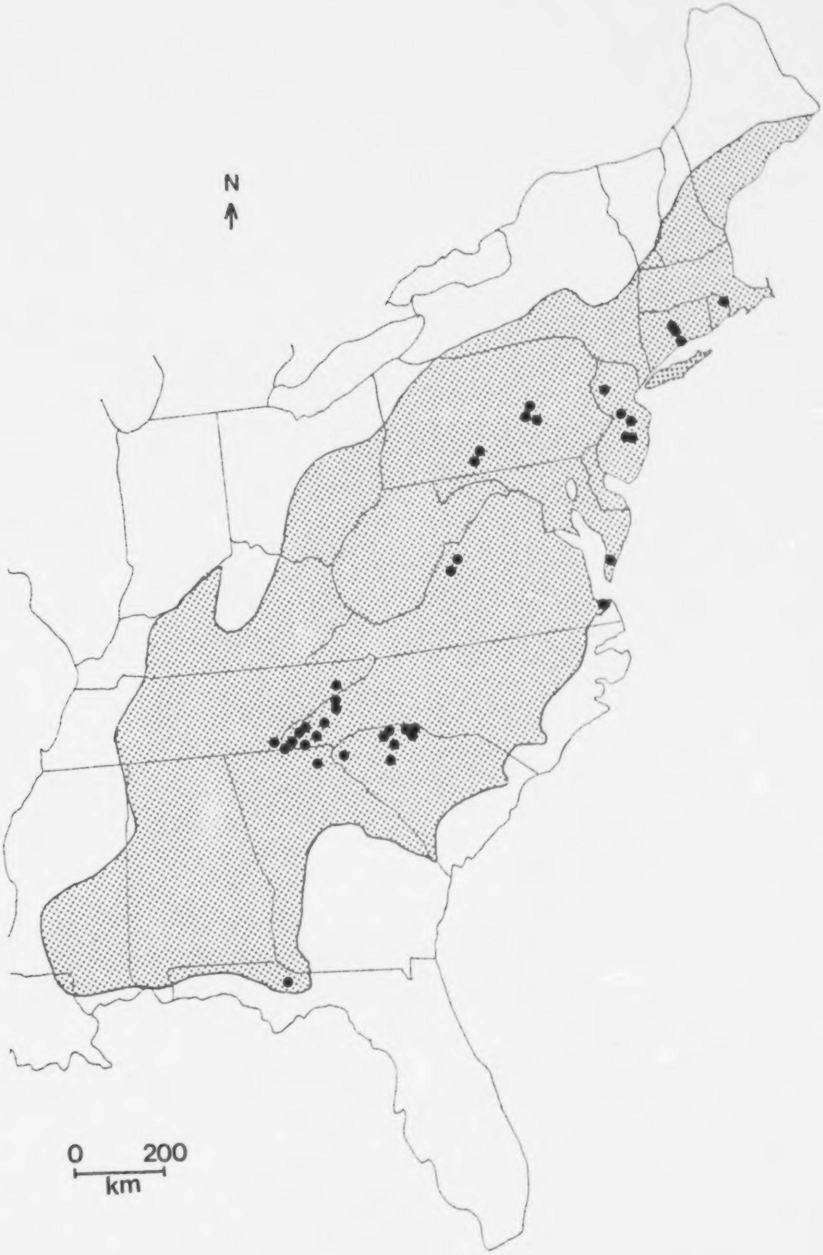


Figure 17. Distribution of *Kalmia latifolia* (dotted area) in eastern United States. (After Ebinger 1988a). Collections used in the flavonoid analyses are indicated by filled circles.

Kalmia polifolia microphylla (Hook.) Piper, Fl. Northwest Coast 282. 1915. *Kalmia polifolia* ssp. *microphylla* (Hook.) Calder & Taylor, Can. J. Bot. 43: 1398. 1965. **Type**: swamps in the Rocky Mountains, *Drummond* (K).

Kalmia occidentalis Small, N. Amer. Fl. 29: 53. 1914. *Kalmia polifolia* ssp. *occidentalis* (Small) Abrams, Ill. Fl. Pacific St. 3: 302. 1951. *Kalmia microphylla* var. *occidentalis* (Small) Ebinger, Rhodora 76: 340. 1974. *Kalmia microphylla* ssp. *occidentalis* (Small) Taylor & MacBryde, Can. J. Bot. 56: 186. 1978. Type: Washington: Foothills of Mt. Rainier, 1883, *Mrs. Bailey Willis* (NY: No.9966!).

Kalmia microphylla var. *occidentalis* f. *alba* Ebinger, Rhodora 76: 342. 1974. Type: Alaska: near Wrangell, *Mrs. J. C. Dart*, 1922. (Holotype: US #1,118,961).

An evergreen shrub 5-60 cm tall, spreading to ascending, usually matted, sparsely branched. Twigs terete, or slightly two angled right below the node, glabrous to lightly pubescent. Leaves opposite; blade ovate to oval to narrowly lanceolate, 4-40 mm long, 3-12 (-18) mm wide, coriaceous; apex obtuse to acute; base obtuse to cuneate; margins flat to slightly revolute; adaxial surface dark green, glabrous or lightly puberulent towards the base; abaxial surface whitened, puberulent; petioles lacking to 2 mm long, glabrous or puberulent. Inflorescence a one to a few flowered, terminal racemose cluster. Pedicels 1-3 cm long, glabrous, subtended by a pair of bracteoles, 2-3 mm long, with ciliated margins, in the axil of a lanceolate leaf-like bract. Calyx pink to light green, 5-10 mm in diameter; lobes ovate, obtuse, 2.7-3.6 mm long, with ciliate margins. Corolla reddish-purple to pink, rarely white, 8-20 mm in diameter, 7-9 mm long. Filaments 3-4.5 mm long; anthers purple, 0.6-1.6 mm long. Style 4.5-7 mm long. Fruit subglobose, 4-7 mm broad, 3.5-6 mm long, glabrous. Seeds winged, oblong, 0.5-1.4 mm long. Chromosome number N = 12.

Distribution and Habitat: This species is distributed in western North America, from California east to Colorado, north to Yukon and Northwest Territories, extending east to the western rim of Hudson Bay of Manitoba and Ontario (Fig. 18). Riley and Walshe (1985) reported the Ontario record of *K. microphylla* which was verified in this study. It is common in open bogs and alpine meadows. Flowering is from July through August.

Common Names: Alpine Laurel, Small-leaved Kalmia, Western Swamp Kalmia, Western Bog Laurel.

Discussion: *Kalmia microphylla* is very closely related to *K. polifolia* and there is no general agreement on the taxonomic treatment of these two taxa (Table 3). The present study shows that the two taxa have quite different flavonoid profiles and are distinctly separated by the multivariate analyses (Figs. 7 and 9, Appendix 5, C). The controversial Pacific lowland (Washington to Alaska) entity "occidentalis" resembles *K. polifolia* in structural features, and has been treated as *K. polifolia* by many taxonomists (Table 3). The present study indicates that this entity is closely related to the "typical microphylla" form and the two together should be recognized as a distinct species. The reliable morphological character which separates *K. microphylla* and *K. polifolia* is the clavate gland on the midribs of both surfaces: the glands are absent in the former and present in the latter (Boivin 1968, Ebinger 1974). Seed size appears to be another useful character: seeds of *K. polifolia* are 1.5-2.2 mm long, while the seeds of *K. microphylla* are less than 1.3 mm long (Ebinger 1974). *Kalmia microphylla* is separate from *K. polifolia* geographically (Fig. 18). I have searched for *Kalmia* in the areas where these two species are distributed close to each other in northeast Manitoba

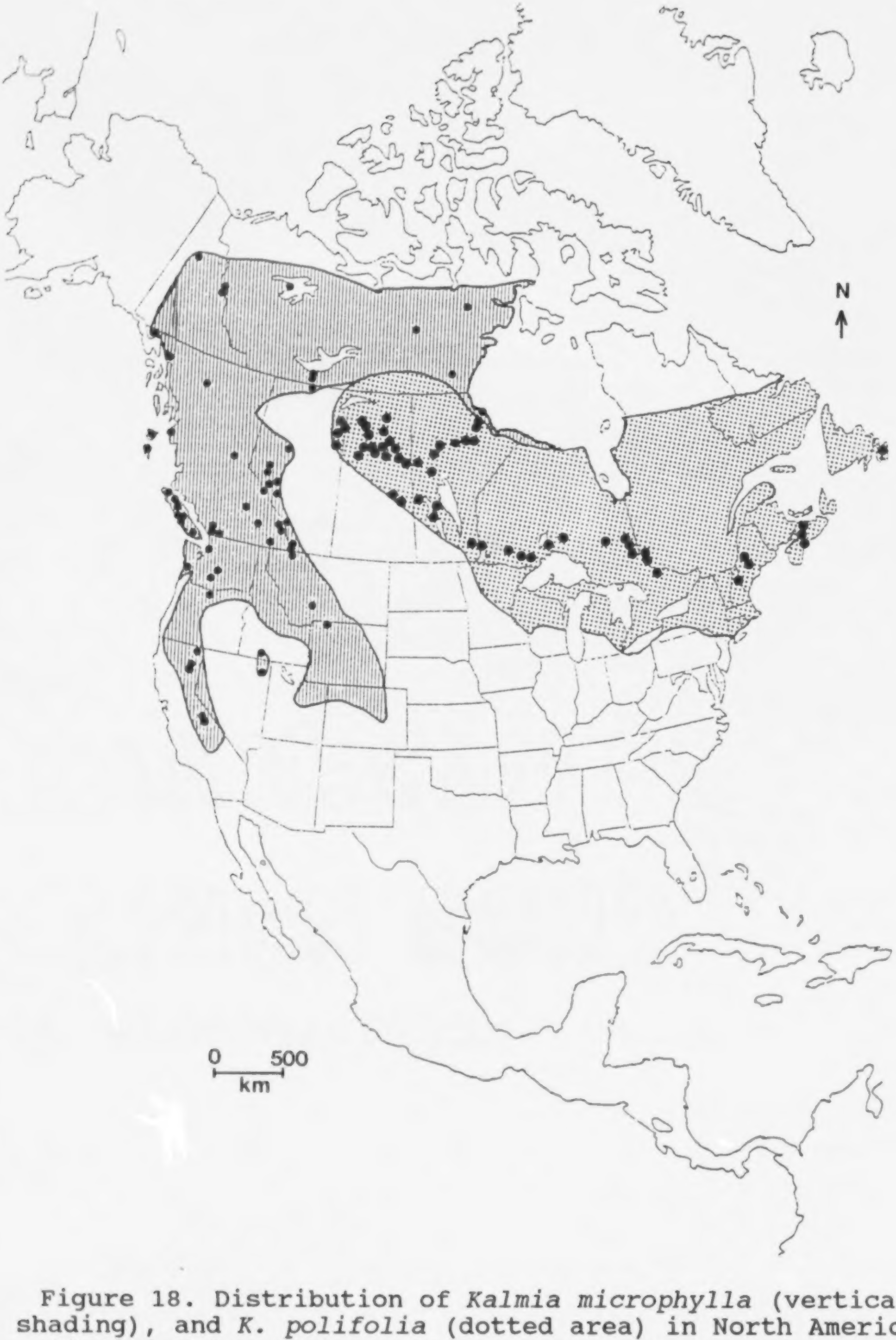


Figure 18. Distribution of *Kalmia microphylla* (vertical shading), and *K. polifolia* (dotted area) in North America. (Modified from Ebinger 1988a). Collections used in the flavonoid analyses are indicated by filled circles.

(walking along the railway track in the Churchill area) and Alberta during summers of 1990 and 1992 without success. *Kalmia microphylla* is a quite variable species, being treated either as two species (Small 1914; see Table 3), two subspecies (Taylor and MacBryde 1978) or two varieties (e.g. Ebinger 1974). The present study indicates that the Pacific lowland (from Washington to Alaska) populations are hardly separable from the alpine populations (Figs. 8 and 9, Appendix 5, D). There exist so many intermediate types in morphology that all populations are better treated as a single variable species with two chemotypes (discussed in Chapter 3).

7. ***Kalmia polifolia*** Wang., Schr. Ges. naturf. Fr. Berlin 8(3): 130. 1788.

Type: unknown.

Kalmia glauca Loddiges ex Ludwig, Neu. Wilde Baumz. 25. 1783. (nom. nud.). *Kalmia glauca* Ait. Hort. Kew. 2: 64. 1789. *Chamaedaphne glauca* O. Kuntze, Rev. Gen. Pl. 2: 388. 1891. Type: Newfoundland (K).

Kalmia polifolia Ludwig, Neu. Wilde Baumz. 25. 1783. (nom. nud.).

Kalmia rosmarinifolia Dum.-Cours. Bot. Cult. 2: 250. 1802. *Kalmia glauca β ? rosmarinifolia* (Dum.-Cours.) Pers. Syn. Pl. 1: 477. 1805. *Kalmia glauca* var. *rosmarinifolia* (Dum.-Cours.) Lavallée, Arbor. Segrez. 159. 1877. Type: unknown.

Kalmia oleaefolia Dum.-Cours. Bot. Cult. 2nd ed. 3: 322. 1811. (as synonym).

Kalmia glauca β rosmarinifolia Pursh, Fl. Am. Sept. 297. 1814. *Kalmia glauca* var. *rosmarinifolia* (Pursh) Jäger, Ziergehölze 279. 1865. *Kalmia polifolia* var. *rosmarinifolia* (Pursh) Rehd. *In* Bailey, Stand. Cyclop. Hort. 3: 1734. 1915. Type: New York: bog near Albany (no designation of types).

Kalmia lanceolata Raf. Autikon Bot. 86. 1840. Type: unknown.

Kalmia glauca var. *superba* Makoy ex Bosse, Vollst. Handb. Blumengart. 2: 348. 1841. (nom. nud.). *Kalmia superba* K. Koch, Dendrologie 2(1): 154. 1872. (nom. nud.).

Kalmia glauca var. *stricta* Jäger, Ziergehölze 279. 1865. Type: unknown.

Kalmia glauca var. *praecox* Lavallée, Arbor. Segrez. 159. 1877. (nom. nud.)

Kalmia polifolia var. *rosmarinifolia* Rehd. *In* Bailey, Cyclop. Amer. Hort. 2: 854. 1900. (without basionym).

Kalmia polifolia f. *leucantha* Schofield & Smith, Can. Field Nat. 67: 94. 1953. Type: Newfoundland: near Hodgewater Line, Trinity South, *E.E. Smith* and *A.C. Smith* 1055 (ACAD).

An evergreen shrub to 1 m tall, sparsely branched. Twigs slightly flattened, two angled, glabrous to puberulent. Leaves opposite; blade oblong to linear, sometimes oval, 1.5-4.5 cm long, 3-15 mm wide, coriaceous; apex obtuse to acute; base obtuse to cuneate; margins usually revolute; adaxial surface dark green; abaxial surface whitened, puberulent; midribs on both surfaces covered with purple clavate trichomes; petioles almost lacking to 3 mm long, with the base ciliate. Inflorescence a one to a few-flowered, terminal raceme. Pedicels 1.5-3 cm long, glabrous, subtended by a pair of bracteoles 2.5-3.5 mm long, with ciliated margins, in the axil of a lanceolate leaf-like bract. Calyx colourless to light pink, 5-7 mm in diameter; lobes ovate, obtuse, 2.9-4.0 mm long, with ciliate margins. Corolla rose-purple, pink, rarely white, 12-18 mm in diameter, 9-11 mm long. Filaments 4-5 mm long; anthers purple, 1-1.5 mm long. Style 4.5-7 mm long. Fruit subglobose, 4-7 mm broad, 4-6 mm long, glabrous. Seeds winged, oblong, 1.5-2.2 mm long. Chromosome number N = 24.

Distribution and Habitat: *Kalmia polifolia* has a wide distribution, from northeastern Alberta east to

Newfoundland, and south to eastern Pennsylvania, and New Jersey (Fig. 18). It is common in open bogs, swamps, and wet areas. Flowering is from May through July.

Common Names: Bog Laurel, Bog Myrtle, Swamp laurel, Pale Laurel, Gold Withy, and American Laurel.

Discussion: No type of *K. polifolia* has been located and the species was described from plants growing in the Tegel Plantation, Berlin (Southall and Hardin 1974). According to Ebinger (1974), Wangenheim's description, illustration, and the distribution discussion of the species were undoubtedly referred to *K. polifolia*. This species is very closely related to *K. microphylla* and they have received many different treatments (Table 3). The results of the present study clearly show that the two species are well separated (Figs. 7 and 9, Appendix 5, C) and there are reliable morphological characters which separate them (see discussion under *K. microphylla*).

Excluded Names

Kalmia spuria Bartr. Trav. 303. 1791; ed. 2, 301. 1792. nom. nud. (probably = *Kalmia hirsuta*).

Kalmia serotina Hoffmgg. Verz. Pflanzenkulturen 70. 1824. nom. nud. (= *Kalmia latifolia* ?).

References

Abrams, L. 1951. *Ericaceae In* Illustrated Flora of the Pacific States: Washington, Oregon and California. Vol. 3, pp. 297-331. Stanford.

Aiton, W. 1789. Hortus Kewensis. Vol.2. London.

Albee, B.J., L.M. Shultz, and S. Goodrich. 1988. *Ericaceae. In* Atlas of the Vascular Plants of Utah. pp. 258-261. Utah Museum of Natural History Occasional Pub. No.7.

Alston, R.E. and B.L. Turner. 1959. Applications of paper chromatography to systematics: recombination of parental biochemical components in a *Baptisia* hybrid population. Nature 184: 285-286.

Alston, R.E. and B.L. Turner. 1963. Biochemical Systematics. Prentice-Hall, Englewood Cliffs, New Jersey.

Anderberg, A.A. 1992. The circumscription of the *Ericales*, and their cladistic relationships to other families of "higher" dicotyledons. Syst. Bot. 17: 660-675.

Anderberg, A.A. 1993. Cladistic interrelationships and major clades of the *Ericales*. Pl. Syst. Evol. 184: 207-231.

Anderson, J.P., Jr. and F.E. Egler. 1988. Patch studies in the stability of non-diversity: *Dennstaedtia*, *Solidago*, *Spiraea*, *Kalmia*. Phytologia 64: 349-364.

Anonymous. 1981. Kalm, Peter. *In* The Encyclopedia Americana, International Edition. Vol. 16, p. 285. Grolier Incorporated, Danbury, Connecticut.

Ashlee, T.R. 1932. A contribution to the Latah flora of Idaho. Northwest Science 6(1): 69-82.

Axelrod D.I. and P.H. Raven. 1985. Origins of the Cordilleran flora. J. Biogeog. 12: 21-47.

Barnhart, J.H. (Compiler). 1965. Kalm, Pehr. *In* The New York Botanical Garden: Biographical Notes upon Botanists. Vol. 2. G.K. Hall & Co., Boston.

Barton, B.S. 1802. Some accounts of the poisonous and injurious honey of North America. Trans. Amer. Philos. Soc. 5: 51-70.

Bate-Smith, E.C. 1962. The phenolic constituents of plants and their taxonomic significance. I. Dicotyledons. J. Linn. Soc. (Bot.) 58: 95-173.

Bate-Smith, E.C. 1968. The phenolic constituents of plants and their taxonomic significance. II. Monocotyledons. J. Linn. Soc. (Bot.) 60: 325-356.

Bayer, R.J. 1989. A systematic and phytogeographic study of *Antennaria aromatica* and *A. densifolia* (*Asteraceae*: *Inuleae*) in the Western North American Cordillera. Madroño 36: 248-259.

Benson, A.B. 1937. The America of 1750: Peter Kalm's travels in North America; The English version of 1770, revised and edited. In two volumes. Wilson-Erickson, Inc., New York. (Note: there is also a 1966 edition by H.N. Benson, published by Dover Publications, Inc. New York).

Benson, G.T. 1930. *Ericaceae*. *In* The trees and shrubs of western Oregon. pp. 128-143. Standford Univ. Press.

Berazain, R. and B.E. Sorribes. 1987. El género *Kalmia* L. (*Ericaceae*) en Cuba. Revista del Jardĩn Botãnico Bacional VIII: 3-17.

Bisby, F.A., J.G. Vaughan, and C.A. Wright. (Eds.). 1980. Chemosystematics: principles and practice. Academic Press, London.

Böcher, T. W. 1981. Evolutionary Trends in Ericalean Leaf Structure. Danske Videnskabernes Selskab Biologiske Skrifter 23(2): 1-64.

Bohm, B.A. 1987. Intraspecific Flavonoid Variation. Bot. Rev. 53: 197-279.

Bohm, B.A. 1988. The minor flavonoids. *In* J.B. Harborne (ed.) The Flavonoids: Advances in research since 1980. pp. 329-388. Chapman and Hall.

Bohm, B.A., S.T. Brim, R.J. Hebda, and P.S. Stevens. 1978. Generic limits in the tribe *Cladothamneae* (*Ericaceae*), and its position in the *Rhododendroideae*. Jour. Arnold Arboretum 59: 311-341.

Bohm, B.A., H.M. Banek, and J.R. Maze. 1984. Flavonoid variation in North America *Menziesia* (*Ericaceae*). Syst. Bot. 9: 324-345.

Bohm, B.A. and J.E. Averett. 1989. Flavonoids in some *Monotropoideae*. Biochem. Syst. Ecol. 17: 399-401.

Boivin, B. 1968. *Ericaceae In* Flora of the Prairie Provinces. Phytologia 16: 3-10.

Borhidi, A. 1985. Phytogeographic Survey of Cuba: I. The Phytogeographic Characteristics and Evolution of the the Flora of Cuba. Acta Bot. Hungarica 31: 3-34.

Borhidi, A. and O. Muñiz. 1986. The Phytogeographic Survey of Cuba: II. Floristic Relationships and Phytogeographic Subdivision. Acta Bot. Hungarica 32: 3-48.

Bourquelot, E. and A. Fichtenholz. 1912. Identification du glucoside des feuilles de *Kalmia latifolia* avec l'asébotine. C.R. Acad. Sci. Paris 154: 526-528.

Bridel, M. and A. Kramer. 1931. Sur la constitution de l'asébotoside (asébotine). Son identité avec le phlorizoside (phlorizine). Cir. Acad. Sci. 193: 748-750.

Britton, N.L. 1908. *Ericaceae. In* North American Trees. pp. 750-764. Archibald Constable & Co. Ltd., London.

Britton, N.L. 1920. Description of Cuban plants new to science. Mem. Torrey Bot. Club 16: 57-118.

Britton, N.L. and A. Brown. 1913. *Ericaceae. In* Illustrated Flora of the Northern United States, Canada and the British Possessions. 2nd ed., Vol.2, pp. 675-694. Charles Scribner's Sons, New York.

Brown, J.H. and A.P. Gibson. 1983. Biogeography. The C.V. Mosby Company. 643 p.

Brown, R.W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. Geological Survey Professional Paper 375: 1-119, with 69 plates. United States Government Printing Office, Washington.

Budantsev, L.Y. 1992. Early stages of formation and dispersal of the temperate flora in the Boreal region. Bot. Rev. 58: 1-48.

Burke, J.W., R.W. Doskotch, C.Z. Ni, and J. Clardy. 1989. Kalanol, a pharmacologically active diterpenoid with a new ring skeleton from *Kalmia angustifolia* L. J. Am. Chem. Soc. 3: 5831-5833

Burke, J.W. and R.W. Doskotch. 1990. High field ^{1}H_ and ^{13}C_NMR assignments of grayanotoxins I, IV, and XIV isolated from *Kalmia angustifolia*. J. Nat. Prod. 53: 131-137.

Cain, S.A. 1944. Foundations of plant geography. Harper and Brothers, New York.

Calder, J.A. and R.L. Taylor. 1965. New taxa and nomenclatural changes with respect to the flora of Queen Charlotte Islands, British Columbia. Can. J. Bot. 43: 1387-1400.

Calder, J.A. and R.L. Taylor. 1968. *Ericaceae*. *In* Flora of the Queen Charlotte Islands. Part I, pp. 453-473. Research Branch, Can. Dept. of Agr. Monogr. No.4.

Camp, W.H. 1947. Distribution patterns in modern plants and the problems of ancient dispersals. Ecol.Monog. 17: 159-183.

Chaney, R.W. 1947. Tertiary centers and migration routes. Ecol. Monogr. 17: 139-148.

Chenon, L.J. 1751. Dissertation Botanica, qua Nova Plantarum Genera. Upsaliae.

Chesters, K.I.M., F.R. Gnauck, and N.F. Hughes. 1967. *Angiospermae*. *In* The Fossil Record, pp. 269-288. Geological Society of London.

Clawson, A.B. 1933. Alpine *Kalmia* (*Kalmia microphylla*) as a stock-poisoning plant. U.S. Dept. Agr. Tech. Bull. 391: 1-9.

Collinson, M. E. and P.R. Crane. 1978. *Rhododendron* seeds from the Paleocene of Southern England. Bot. J. Linn. Soc. 76: 195-205.

Cooper, S.D. and J.B. McGraw. 1988. Constraints on reproductive potential at the level of the shoot module in three ericaceous shrubs. Functional Ecology 2: 97-108.

Copeland, H.F. 1943. A study, anatomical and taxonomic of the genera *Rhododendroideae*. Amer. Midl. Nat. 30: 533-625.

Cox, H.T. 1948. Studies in the comparative anatomy of the *Ericales* I. *Ericaceae* --- subfamily *Rhododendroideae*. Amer. Midl. Nat. 39: 220-245.

Crawford, D.J. 1978. Flavonoid chemistry and angiosperm evolution. Bot. Rev. 44: 431-456.

Crawford, D.J. 1990. Plant Molecular Systematics. New York: John Wiley & Sons.

Crawford, D.J. and D.E. Giannasi. 1982. Plant Chemosystematics. BioScience 32: 114-124.

Cronquist, A. 1980. Chemistry in plant taxonomy: an assessment of where we stand. *In* F.A. Bisby, J.G. Vaughan, and C.A. Wright (eds.). Chemosystematics: principles and practice. pp. 1-27. Academic Press, London.

Cronquist, A. 1981. *Ericaceae*. *In* An integrated system of classification of flowering plants. pp. 479-483. Columbia University Press.

Cullings, K.W. and T.D. Bruns. 1992. Phylogenetic origin of the *Monotropoideae* inferred from partial 28S ribosomal RNA gene sequences. Can. J. Bot. 70: 1703-1708.

Czekalski, M. 1985. Mountain laurel (*Kalmia latifolia* L.) in Poland. Rocznik Dendrologiczny 36: 61-72.

Daubenmire, R. 1978. Evolution of North America Vegetation. *In* Plant Geography, pp. 48-65. Academic Press.

Davis, R.J. 1952. *Ericaceae*. *In* Flora of Idaho. pp. 528-533. WM. C. Brown Company Publishers, Dubuque, Iowa.

Dayton, W.A. 1931. Important Western Browse Plants. United States Dept. of Agr. Miscellaneous Publication No. 101. Washington, D.C., 214 p.

Delcourt, H.R., P.A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. Quaternary Sci. Rev. 1: 153-175.

Delcourt, P.A. and H.R. Delcourt. 1981. Vegetation maps for eastern North America: 40,000 B.P. to the present. *In* R.C. Romans (ed.), Geobotany II, pp. 123-157.

Delcourt, P.A. and H.R. Delcourt. 1983. Late-Quaternary vegetational dynamics and community stability reconsidered. Quaternary Research 19: 265-271.

Delcourt, P.A. and H.R. Delcourt. 1987. Late-Quaternary dynamics of temperate forests: applications of paleoecology to issues of global environmental change. Quaternary Sci. Rev. 6: 129-146.

Denford, K.E. 1973. Flavonoids of *Arctostaphylos uva-ursi* (*Ericaceae*). Experientia 29: 939.

Denford, K.E. 1981. Chemical subdivisions within the genus *Arctostaphylos* based on flavonoid profiles. Experientia 37: 1287-1288.

Denford, K.E. 1984. Phytochemical approaches to biosystematics. *In* W.F. Grant (ed.). Plant Biosystematics. pp. 359-376. Academic Press, Toronto.

Denford, K.E. and I. Karas. 1975. A study of the flavonoids of certain species of *Cassiope* (*Ericaceae*). Can. J. Bot. 53(12): 1192-1195.

Dorn, R.D. 1977. *Ericaceae*. *In* Manual of the Vascular Plants of Wyoming. Vol.I. pp. 654-669. Garland Publishing, Inc., New York.

Douglas, S. 1983. Floral colour patterns and pollinator attraction in a bog habitat. Can. J. Bot. 61: 3494-3501.

Downie, S.R. 1987. A biosystematic study of *Arnica* subgenus *Arctica*. Ph.D. dissertation, University of Alberta, Edmonton.

Downie, S.R. and K.E. Denford. 1986. The flavonoids of *Arnica frigida* and *A. louiseana* (*Asteraceae*). Can. J. Bot. 64: 2748-2752.

Doyle, K.M., T.J. Fahey, and R.D. Paratley. 1987. Subalpine heathlands of Mahoosuc Range, Maine. Bull. Torrey Bot. Club 114(4): 429-436.

Dudley, T.R. 1967. Ornamental mountain-laurel and a new cultivar: *Kalmia latifolia* 'Bettina'. Amer. Hort. Mag. 46: 245-248.

Duppstadt, W.H. 1980. Update on New and Noteworthy Plant Collection for West Virginia. Proc. W. VA. Acad. Sci. 52(2): 93-94.

Ebinger, J.E. 1974. A systematic study of genus *Kalmia*. Rhodora 76: 315-398.

Ebinger, J.E. 1988a. Laurels in the wild. *In* R.A. Jaynes, *Kalmia* The Laurel Book II, Chapter 2, pp 15-42. Timber Press, Portland, Oregon.

Ebinger, J.E. 1988b. Medicinal uses and toxicity of laurel foliage. *In* R.A. Jaynes, *Kalmia* The Laurel Book II, Chapter 10, pp 159-165. Timber Press, Portland, Oregon.

Elias, T.S. 1980. The Complete Trees of North America, Field Guide and Natural History. Outdoor Life/Nature Books, New York.

El-Naggar, S. F., F.S. El-Feraly, J.S. Foos, and R.W Doskotch. 1980. Flavonoids from the leaves of *Kalmia latifolia*. J. Nat. Prod. 43: 739-751.

El-Naggar, S.F., R.W. Doskotch, T.M. O'Dell, and L. Girard. 1980. Antifeedant diterpenes for the gypsy moth larvae from *Kalmia latifolia*: isolation and characterization of ten grayanoids. J. Nat. Prod. 43: 617-631.

Espejel, I. 1987. A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula. J. Biogeog. 14: 499-519.

Estrada-Loera, E. 1991. Phytogeographic relationships of the Yucatán Peninsula. J. Biogeog. 18: 687-697.

Fernald, M.L. 1937. Local plants of inner coastal plain of southeastern Virginia. Rhodora 39: 321-366, 379-415, 433-459, 465-491 + Errata p. 498.

Fernald, M.L. 1950. *Ericaceae*. *In* Gray's Manual of Botany. 8th ed. pp. 1114-1135. American Book Company.

Fernald, M.L. 1970. *Ericaceae*. *In* Gray's Manual of Botany. 8th ed. with corrections supplied by R.C. Rollins. pp. 1114-1135. D. Van Nostrand Company.

Foss, P.J. and G.J. Doyle. 1988. A palynological study of the Irish *Ericaceae* and *Empetrum*. Pollen et Spores, Vol. XXX: 151-178.

Foster, D.R., H.E. Wright, Jr., M. Thelaus, and G.A. King. 1988. Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. J. Ecol. 76: 1164-1185.

Friis, E.M., W.G. Chaloner, and P.R. Crane. (Eds.). 1987. The origins of Angiosperms and their biological consequences. Cambridge University Press.

Fulton, R.J. (Ed.). 1989. Quaternary Geology of Canada and Greenland. Geological Survey of Canada, Geology of Canada, no. 1.

Ganapathy, P.S. and B.F. Palser. 1964. Studies of Floral Morphology in the *Ericales*. VII. Embryology in the Phyllodoceae. Botan. Gaz. 125(4): 280-297.

Giannasi, D.E. 1978. Systematic aspects of flavonoid biosynthesis and evolution. Bot. Rev. 44: 399-429.

Giannasi, D.E. 1988. Flavonoids and evolution in the dicotyledons. *In* J.B. Harborne (ed.) The Flavonoids: Advances in research since 1980. pp. 479-504. Chapman and Hall.

Giannasi, D.E. and D.J. Crawford. 1986. Biochemical Systematics II. A Reprise. Evolutionary Biology 20: 25-248.

Gilkey, H.M. and L.R.J. Dennis. 1975. *Ericaceae. In* Handbook of Northwestern Plants. pp. 296-316. Oregon State Univ. Bookstore, Inc., Corvallis, Oregon.

Gleason, H.A. 1931. Botanical results of the Tyler-Duida Expedition. Bull. Torr. Bot. Club 58: 277-506.

Gleason, H.A. 1952. *Ericaceae In* The New Britton and Brown Illustrated Flora of the Northwestern United States and Adjacent Canada. Vol.3, pp. 2-32. The New York Botanical Garden.

Gleason, H.A. and E.P. Killip. 1939. The flora of Mount Auyan-Tepui, Venezuela. Brittonia 3: 97-204.

Gleason, H.A. and A. Cronquist. 1963. *Kalmia. In* Manual of Vascular Plants of Northeastern United States and Adjacent Canada, p. 527. D. Van Nostrand Company, Inc.

Gleason, H.A. and A. Cronquist. 1991. *Kalmia. In* Manual of Vascular Plants of Northeastern United States and Adjacent Canada. 2nd ed. p. 205. The New York Botanical Garden. New York.

Gornall, R.J. and B.A. Bohm. 1978. Angiosperm flavonoid evolution: A reappraisal. Syst. Bot. 3: 353-368.

Gothan, W. and H. Weyland. 1973. Lehrbuch der Paläobotanik. Akademic-Verlag, Berlin. 677p.

Graham, A. (Ed.). 1972. Floristics and paleofloristics of Asia and eastern North America. Elsevier Publishing Company, Amsterdam.

Graham, A. (Ed.). 1973. Vegetation and vegetational history of northern Latin America. Elsevier Scientific Publishing Company, Amsterdam - London - New York.

Grant, W.F. (Ed.). 1984. Plant Biosystematics. Academic Press, Toronto.

Gray, A. 1870. Dialysis with staminody in *Kalmia latifolia*. Amer. Nat. 4: 373-374.

Greuter, W. and other members of Editorial Committee (eds). 1988. International Code of Botanical Nomenclature. Adopted by the Fourteenth International Botanical Congress, Berlin, July-August 1987. Reg. Veg. 118: 1-328.

Griffith, R.E. 1847. *Ericaceae*. *In* Medical Botany. pp. 423-431. Lea & Blanchard, Philadelphia.

Griffith, R.E. 1848. On poisons, in relation to Medical Jurisprudence and Medicine. Lea & Blanchard, Philadelphia.

Gruezo, W. SM. 1988. A Biosystematic Revision of *Arnica* L. Subgenus *Chamissonis* Maguire. Ph.D. dissertation, University of Alberta, Edmonton.

Guyer, C. and J.M. Savage. 1986. Cladistic relationships among anoles (*Sauria*: *Iguanidae*). Syst. Zool. 35: 509-531.

Haber, E. 1983. Morphological variability and flavonol chemistry of the *Pyrola asarifolia* complex (*Ericaceae*) in North America. Syst. Bot. 8: 277-298.

Haber, E. 1987. Variability, distribution, and systematics of *Pyrola picta* s.l. (*Ericaceae*) in Western North America. Syst. Bot. 12: 324-335.

Haber, E. 1988. Hybridization of *Pyrola chlorantha* (*Ericaceae*) in North America. Can. J. Bot.: 1993-2000.

Haber, E. and H. Takahashi. 1988. A comparative study of the North American *Pyrola asarifolia* and its Asian vicariad, *P. incarnata* (*Ericaceae*). Bot. Mag. Tokyo 101: 483-495.

Hagerup, O. 1928. Morphological and cytological studies of bicornes VI. Dansk Bot. Arkiv. 6: 1-26.

Hagerup, O. 1953. On morphology and systematics of the leaves in *Ericales*. Phytomorphology 3: 459-464.

Hall, H.M. 1912. New and Noteworthy Californian Plants, I. Univ. of Calif. Publ. in Bot. 2(12): 195-208.

Hall, I.V., L.P. Jackson, and C.F. Everett. 1973. The biology of Canadian weeds. 1. *Kalmia angustifolia* L. Can. J. Plant Sci. 53: 865-873.

Hammen, T. van der, T.A. Wijmstra, and W.H. Zagwijn. 1971. The floral record of the Late Cenozoic of Europe. *In* K.K. Turekian (ed.), The Late Cenozoic Glacial Ages, pp. 391-424. Yale University Press.

Harborne, J.B. 1967. Comparative Biochemistry of the flavonoids. Academic Press, London. 383p.

Harborne, J.B. 1969. Gossypetin and Herbacetin as Taxonomic Markers in Higher Plants. Phytochemistry 8: 177-183.

Harborne, J.B. 1972. Evolution and function of flavonoids in plants. *In* Recent advances in Phytochemistry, Vol. 4, pp. 107-141. Appleton-Century-Crafts, New York.

Harborne, J.B. 1977. Flavonoids and the evolution of the angiosperms. Biochem. Syst. & Ecol. 5: 7-22.

Harborne, J.B. 1980a. New experimental approaches to plant chemosystematics. *In* F.A. Bisby, J.G. Vaughan, and C.A. Wright (eds.). Chemosystematics: principles and practice. pp. 39-70. Academic Press, London.

Harborne, J.B. 1980b. Flavonoid pigments as both taxonomic and phyletic markers in the genus *Rhododendron*. *In* J.L. Luteyn and M.E. O'Brien (eds) Contributions toward a classification of *Rhododendron*. pp. 145-161. The New York Botanical Garden.

Harborne, J.B. (Ed.). 1988. The Flavonoids: Advances in research since 1980. Chapman and Hall, London & New York. 621p.

Harborne, J.B. 1989. General procedures and measurement of total phenolics. *In* Methods in Plant Biochemistry, Vol.1, pp. 1-28. Academic Press.

Harborne, J.B. 1991. The first thirty years--phytochemists past and present. Phytochemistry 30: 3852-3855.

Harborne, J.B. and C.A. Williams. 1971. Leaf survey of flavonoids and simple phenols in the genus *Rhododendron*. Phytochemistry 10: 2727-2744.

Harborne, J.B. and C.A. Williams. 1973. A chemotaxonomic survey of flavonoids and simple phenols in leaves of the *Ericaceae*. Bot. J. Linn. Soc. 66: 37-54.

Harborne, J.B., T.J. Mabry, and H. Mabry. (Eds.). 1975. The Flavonoids. Chapman and Hall, London. 1204p.

Harborne, J.B. and T.J. Mabry. (Eds.). 1982. Flavonoids: Advances in Research, 1975-1980. Chapman and Hall, London.

Harborne, J.B. and B.L. Turner. 1984. Plant Chemosystematics. Academic Press, London. 562p.

Harrington, H.D. 1954. *Ericaceae. In* Manual of the Plants of Colorado: For the Identification of the Ferns and Flowering Plants of the State. pp. 415-420. Denver, Sage Books.

Harrington, H.D. 1964. *Ericaceae. In* Manual of the Plants of Colorado: For the Identification of the Ferns and Flowering Plants of the State. pp. 415-420. Denver, Sage Books.

Heisey, R.M. and B.K. Gorham. 1992. Antimicrobial effects of plant extracts on *Streptococcus mutans*, *Candida albicans*, *Trichophyton rubrum* and other microorganisms. Letters in Applied Microbiology 14(4): 136-139.

Heller, A.A. 1898. New and interesting plants from Western North America. -III. Bull. Torrey Bot. Club 25: 580-582.

Henderson, L.F. 1931. New Plants from Oregon. Rhodora 34: 203-206.

Heywood, V.H. (Ed.). 1978. *Ericaceae. In* Flowering plants of the world, pp. 124-127. Mayflower Books.

Hickey, L.J. 1977. Stratigraphy and Paleobotany of the Golden Valley Formation (Early Tertiary) of Western North Dakota. The Geological Society of America, Inc., Memoir 150: 1-181 + 55 plates.

Hinds, H.R. 1986. *Ericaceae In* Flora of New Brunswick. pp. 315-320. Primrose Press, Fredericton, N.B.

Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1959. *Ericaceae*. *In* Vascular plants of the Pacific Northwest. Part 4, pp. 1-36. Univ. of Washington Press, Seattle.

Hitchcock, C.L. and A. Cronquist. 1973. *Ericaceae*. *In* Flora of the Pacific Northwest, an Illustrated Manual. pp. 340-350. Univ. of Washington Press. Seattle & London.

Hollik, A. 1892. Additions to the Paleobotany of the Cretaceous formation of Staten Island. Trans. N.Y. Acad. Sci. 12: 28-39.

Hollik, A. 1931. Plant remains from a Pleistocene lake deposit in the Upper Connecticut River Valley. Brittonia 1: 35-56.

Holmes, M.L. 1956. *Kalmia*, the American Laurels. Baileya 4: 89-94.

Hooker, W.J. 1834. *Kalmia*. *In* Flora Boreali-Americana; or, the Botany of the Northern Parts of British America. Vol II, Part 7, p. 41. London.

Hultén, E. 1945. *Kalmia In* Flora of Alaska and Yukon. Vol.5, pp. 1229-1231. Lund.

Hultén, E. 1968. *Ericaceae*. *In* Flora of Alaska and neighbouring Territories. pp. 717-736. Stanford Univ. Press.

Huntley, B. and T. Webb, III. (Eds.). 1988. Vegetation History. Kluwer Academic Publishers.

Hutchinson, J. 1973. *Ericaceae*. *In* The flowering plants arranged according to a new system based on their probable phylogeny. pp. 356-358. Oxford at the Clarendon Press.

Ikuse, M. 1954. The presence of the viscid threads among pollen grains in *Phyllodoceae*, etc. of *Ericaceae*. Journ. Jap. Bot. 29(5): 146-148.

Ismail, A.A. and D.E. Yarborough. 1981. Lambkill control in lowbush blueberry fields with glyphosate and 2,4-D. J. Amer. Soc. Hort. Sci. 106: 393-396.

Ives, J.D. 1974. Biological refugia and the nunatak hypothesis. *In* J.D. Ives and R.G. Barry (eds.). Arctic and Alpine, pp. 605-636. Methuen.

Jacobson, G.L., Jr., T. Webb III, and E.C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. *In* W.F. Ruddiman and H.E. Wright, Jr. (eds). North America and adjacent oceans during the last deglaciation, pp. 277-288 + 2 plates. Boulder, Colorado: Geological Society of America, The Geology of America, v. K-3.

James, F.C. and C.E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or pandora's box? Annu. Rev. Ecol. Syst. 21: 129-166.

Jankowski, K. and J.R.J. Paré. 1983. Trace glycoside from cranberries (*Vaccinium oxyccocus*). J. Nat. Prod. 46: 190-193.

Jaynes, R.A. 1968a. Interspecific crosses in *Kalmia*. Amer. J. Bot. 55(9): 1120-1125.

Jaynes, R.A. 1968b. Self Incompatibility and Inbreeding Depression in Three Laurel (*Kalmia*) species. Proceedings of the American Society for Horticultural Science. 93: 618-622.

Jaynes, R.A. 1968c. Breaking seed dormancy of *Kalmia hirsuta* with high temperatures. Ecology 49(6): 1196-1198.

Jaynes, R.A. 1969. Chromosome counts of *Kalmia* species and revaluation of *K. polifolia* var. *microphylla*. Rhodora 71: 280-284.

Jaynes, R.A. 1970. Breeding ornamental mountain laurel. HortScience 5(4): 344.

Jaynes, R.A. 1971a. Selection of propagation of improved *Kalmia latifolia* cultivars. Proceedings of the international plant propagators Society Annual Meeting. 1971. pp. 366-373.

Jaynes, R.A. 1971b. The *Kalmia* and their hybrids. The Quarterly Bulletin of the American *Rhododendron* Society, July 1971. pp. 1-5.

Jaynes, R.A. 1971c. A gene controlling pigmentation in sheep laurel. J. Hered. 62: 201-203.

Jaynes, R.A. 1971d. Laurel selections from seed: True breeding red-budded mountain laurel. Circular of the Connecticut Agricultural Experiment Station, New Haven, No. 240: 1-10.

Jaynes, R.A. 1973. Inheritance of three forms of mountain laurel. HortScience 8(3): 269.

Jaynes, R.A. 1974. Inheritance of Flower and Foliage characteristics in Mountain Laurel (*Kalmia latifolia* L). J. Amer. Soc. Hort. Sci. 99(3): 209-211.

Jaynes, R.A. 1975. The Laurel Book--Rediscovery of the North America Laurels. Hafner Press, New York. 180p.

Jaynes, R.A. 1978. Inheritance patterns of unusual forms of *Kalmia latifolia*. HortScience 13(3): 388.

Jaynes, R.A. 1981. Inheritance of ornamental traits in mountain laurel *Kalmia latifolia*. J. Hered. 72: 245-248.

Jaynes, R.A. 1988a. *Kalmia*, The Laurel Book II. Timber Press, Portland, Oregon, 220 p.

Jaynes, R.A. 1988b. The taming of a species (and its cultivars). Am. Nurseryman 167(11): 29-32, 34.

Jepson, W.L. 1925. *Ericaceae. In* A manual of the flowering plants of California, pp. 735-752. Associated Students Store, Univ. of California at Berkeley, California.

Jobidon, R. 1991. Control of *Kalmia* with bialaphos, a microbially produced phytotoxin. North J. Appl. For. 8(4): 147-149.

Judd, W.S. 1983. *Kalmia ericoides* revisited. Rhodora 85: 45-54.

Judd, W.S. and K.A. Kron. Circumscription of *Ericaceae* (*Ericales*) as determined by preliminary cladistic analyses based on morphological, anatomical, and embryological features. Brittonia 45: 99-114.

Juel, H.O. and J.W. Harshberger. 1929. New light on the collection of North American plants made by Peter Kalm. Proceedings of the Academy of Natural Sciences of Philadelphia LXXXI: 297-303.

Jussieu, A.L. de. 1789. Genera Plantarum. Paris.

Karlin, E.F. and L.M. Lynn. 1988. Dwarf-shrub bogs of the southern Catskill Mountain region of New York State: Geographic changes in the flora of peatlands in northern New Jersey and southern New York. Bull. Torrey Bot. Club 115: 209-217.

Karlstrom, T.N.V. and G.E. Ball. (Eds.). 1969. The Kodiak Island Refugium: its geology, flora, fauna and history. Ryerson Press, Toronto, 262 p.

Kartesz, J.T. and R. Kartesz. 1980. *Kalmia*. *In* A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. Vol.II, p. 193. The Univ. of North Carolina Press, Chapel Hill.

Kaul, V., J.L. Rouse, and E.G. Williams. 1986. Early events in the embryo sac after intraspecific and interspecific pollinations in *Rhododendron kawakamii* and *R. retusum*. Can. J. Bot. 64: 282-291.

King, B.L. 1977. Flavonoid Analysis of Hybridization in *Rhododendron* Section *Pentanthera* (*Ericaceae*). Syst. Bot. 2: 14-27

King, B.L. 1980. The systematic Implications of Flavonoids in *Rhododendron* Subgenus *Pentanthera*. *In* J.L. Luteyn and M.E. O'Brien (eds.), Contributions toward a Classification of *Rhododendron*. pp. 163-185. The New York Botanical Garden.

Kingsbury, J.M. 1964. *Ericaceae*. *In* Poisonous plants of the United States and Canada. pp. 251-260. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Kirkwood, J.E. 1930. *Kalmia*. *In* Northern Rocky Mountain Trees and Shrubs. pp. 261-263. Stanford Univ. Press.

Kittredge, D.B., Jr. and P.M.S. Ashton. 1990. Natural regeneration patterns in even-aged mixed stands in southern New England. Northern J. Applied Forestry 7(4): 163-168.

Kral, R. 1983. *Ericaceae*: *Kalmia cuneata* Michx. white-wicky laurel. Technical Publication R8-TP-USDA: Forest Service, South Region, Paper 171, pp. 833-836.

Kress, A. 1988. Beobachtungen an blüten von *Kalmia latifolia* L. (*Ericaceae*). Phytologia 65(4): 249-284.

Krutzsch, W. 1989. Paleogeograpy and historical phytogeography (paleochorology) in the Neophyticum. Pl. Syst. Evol. 162: 5-61.

Kuijt, J. 1982. *Ericaceae*. *In* A Flora of Waterton Lakes National Park. pp. 259-273. The Univ. of Alberta Press.

Kunishige, M. and Y. Kobayashi. 1980. Chromatographic identification of Japanese azalea species and their hybrids. *In* J.L. Luteyn and M.E. O'Brien (eds.), Contributions toward a Classification of *Rhododendron*. pp. 277-287. The New York Botanical Garden.

Kuntze, O. 1891. Revisio Generum Plantarum. Part II. Leipzig.

Kurmes, E.A. 1961. The ecology of mountain laurel in southern New England. Unpublished doctoral dissertation, Yale University, New Haven. 85p.

Kurmes, E.A. 1967. Notes and Discussion: the distribution of *Kalmia latifolia* L. The Amer.Midland Naturalist 77: 525-526.

Kurmis, V., S.L. Webb, and L.C. Merriam, Jr. 1986. Plant communities of Voyageurs National Park, Minnesota, U.S.A. Can. J. Bot. 64: 531-540.

Largent, D.L., N. Sugihara, and C. Wishner. 1980. Occurrence of mycorrhizae on ericaceous and pyrolaceous plants in northern California. Can. J. Bot. 58: 2274-2279.

Layser, E.F. 1980. Flora of Pend Oreille County, Washington. Wash. State Univ. Cooperative Extension, Pullman, Washington. 146p.

Leopold, E.B. and H.D. MacGinitie. 1972. Development and Affinities of Tertiary Floras in the Rocky Mountains. *In* A. Graham (ed.). Floristics and paleofloristics of Asia and eastern North America. pp. 145-200. Elsevier Publishing Company, Amsterdam.

Linnaeus, C. 1753. Species Plantarum. Stockholm.

Lipscomb, M.V. and E.T. Nilsen. 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast and southwest slopes of the southern Appalachian Mountains. I. Irradiance tolerance. Amer. J. Bot. 77(1): 108-115.

Lipscomb, M.V. and E.T. Nilsen. 1990b. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast- and southwest- facing slopes of the southern Appalachian Mountains. II. Water relations. Amer. J. Bot. 77(4): 517-526.

Litke, R. 1968. Pflanzenreste aus dem unterminozän in Nordwestsachsen. Palaeontographica Abt. B. 123: 173-183.

Little, E.L. 1979. A check list of United States trees (native and naturalized). Forest Service, U.S. Dept. of Agr., Washington, D.C.

Loudon, J.C. 1842. Genus XXII *Kalmia*. *In* An Encyclopedia of Trees and Shrubs. pp. 598-600. London.

Löve, A. (Ed.). 1982a. IOPB chromosome number reports LXXV. Taxon 31: 342-368.

Löve, A. 1982b. IOPB chromosome number reports LXXVI. Taxon 31: 761-777.

Luteyn, J.L., J.B. Harborne, and C.A. Williams. 1980. A survey of the flavonoids and simple phenols in leaves of *Cavendishia* (*Ericaceae*). Brittonia 32: 1-16.

Lynch, J.D. 1988. Refugia. *In* A.A. Myers and P.S. Giller (eds.). Analytical biogeography: An integrated approach to the study of animal and plant distributions, pp. 311-342. Chapman and Hill.

Lynn, L.M. and Karlin, E.F. 1985. The Vegetation of the low-shrub bogs of northern New Jersey and adjacent New York: Ecosystems at their southern limit. Bull. Torrey Bot. Club 112: 436-444.

Ma, Y.C. (Ed.). 1980. *Ericaceae*. *In* Flora Intramongolica. Vol.5, pp. 6-21. Typis Intramongolicae Popularis, Hulhot.

Mabry, T.J., K.R. Markham, and M.B. Thomas. 1970. The systematic identification of flavonoids. Springer-Verlag, New York. 453p.

Mabry, T.J., M. Sakakibara, and B.L. King. 1975. Asebotin and its aglucone from three species of *Rhododendron*. Phytochemistry 14: 1448-1450.

Maguire, B. 1970. On the Flora of the Guayana Highland. Biotropica 2: 85-100.

Maguire, B., J.A. Steyermark, and J. L. Luteyn. 1978. *Ericaceae*. Mem. New York Bot. Gard. 29: 139-203.

Mai, D.H. 1989. Development and regional differentiation of the European vegetation during the Tertiary. Pl. Syst. Evol. 162: 79-91.

Mai, D.H. 1991. Palaeofloristic changes in Europe and the confirmation of the Arctotertiary-Palaeotropical geofloral concept. Rev. Palaeobot. Palynol. 68: 29-36.

Mallik, A.U. 1987. Allelopathic potential of *Kalmia angustifolia* to black spruce (*Picea mariana*). Forest Ecology and Management 20: 43-51.

Mallik, A.U. 1990. Allelopathy and the competitive advantage of *Kalmia angustifolia* over black spruce. *In* The Silvics and Ecology of Boreal Spruces. 1989 IUFRO Working Party SI. 05-12 Symp. Proc., Newfoundland, 12-17 Aug. 1989. For. Can. Inf. Rep. N-X-271. 203p. Ed. B.D. Titus, M.B. Lavigne, P.F. Newton, and W.J. Meades.

Mallik, A.U. 1991. Cutting, burning, and mulching to control *Kalmia*: results of a greenhouse experiment. Can. J. For. Res. 21: 417-420.

Mallik, A.U. 1993. Ecology of a forest weed of Newfoundland: vegetative regeneration strategy of *Kalmia angustifolia*. Can. J. Bot. 71: 161-166.

Mallik, A.U. and P.F. Newton. 1988. Inhibition of black spruce seedling growth by forest-floor substances of central Newfoundland. Forest Ecology and Management 23: 273-283.

Mancini S.D. and J.M. Edwards. 1979. Cytotoxic Principles from the Sap of *Kalmia latifolia*. J. Nat. Prod., 42: 483-488.

Markham, K.R. 1982. Techniques of flavonoid identification. Academic Press. 113p.

Marsh, C.D. and A.B. Clawson. 1930. Mountain-laurel (*Kalmia latifolia*) and sheep laurel (*Kalmia angustifolia*) as stock-poisoning plants. U.S. Dept. Agr. Tech. Bull. 219: 1-22.

Matthews, J.V., Jr., T.W. Anderson, M. Boyko-Diakonow, R.W. Mathewes, J.H. McAndrews, R.J. Mott, P.J.H. Richard, J.C. Ritchie, and C.E. Schweger. 1989. Quaternary environments in Canada as documented by paleobotanical case histories. *In* Fulton, R.J. (ed.). 1989. Quaternary

Geology of Canada and Greenland, pp. 481-539. Geological Survey of Canada, Geology of Canada, no. 1.

Mckenna, M.C. 1983. Holarctic landmass rearrangement, cosmic events, and Cenozoic terrestrial organisms. Ann. Missouri Bot. Gard.70: 459-489.

Meidinger, D. 1990. *Ericaceae*. *In* E.W. Douglas, G.B. Straley, and D. Meidinger (editors), the Vascular Plants of British Columbia. Part 2. pp. 6-20. B.C. Ministry of Forest.

Monk, C.D., D.T. McGinty, and F.P. Day, Jr. 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. Bull Torrey Bot. Club 112: 187-193.

Moss, E.H. 1983. *Ericaceae*. *In* Flora of Alberta (2nd ed. revised by J.G. Packer). pp. 439-449. Univ. of Toronto Press, Toronto.

Muenscher, W.C. 1940. *Ericaceae*. *In* Poisonous Plants of the United States. pp. 179-185. The Macmillan Company, New York.

Muenscher, W.C.. 1960. *Ericaceae*. *In* Poisonous Plants of the United States. Revised Edition. pp. 182-188. The Macmillan Company, New York.

Muller, R.N. 1991. Growing season water relations of *Rhododendron maximum* L. and *Kalmia latifolia* L. Bull. Torrey Bot. Club 118: 123-127.

Munz, P.A. and D.D. Keck. 1973. *Kalmia*. *In* A California Flora, combined ed. P. 413 (text) and p. 79 (supplement). Univ. of Calif. Press, Berkeley.

Nicholson, G. 1896. Hand-list of trees and shrubs grown in Arboretum. Part II. Gamopetalae to Monocotyledons. Royal Gardens, Kew.

Niklas, K.J. (Ed.). 1981. Paleobotany, Paleoecology, and Evolution. In 2 volumes. Praeger, New York.

Nuttall, T. 1818. *Kalmia*. *In* The Genera of North American Plants, and a Catalogue of the Species, to the year 1817. Vol.I, pp. 267-268. Philadelphia.

Ohwi, J. 1965. *Ericaceae*. *In* Flora of Japan, pp. 693- 712. Smithsonian Institution, Washington, D.C.

O'Keefe, J.F. 1981. Factors affecting the distribution and growth of mountain laurel (*Kalmia latifolia*) in central Massachusetts. MS Thesis, University of Massachusetts, Amherst.

Oliver, E.G.H. 1991. The *Ericoideae* (*Ericaceae*) - a review. Contributions from the Bolus Herbarium 13: 158-208.

Packer, J.G. and K.E. Denford. 1974. A contribution to the taxonomy of *Arctostaphylos uva-ursi*. Can. J. Bot. 52: 743-753.

Packer, J.G. and D.H. Vitt. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Can. J. Bot. 52: 1393-1409.

Pammel, L.H. 1911. *Ericaceae*. *In* A manual of Poisonous Plants. pp. 664-675. The Torch Press, Cedar Rapids, Iowa.

Parmelee, J.A. and J. Ginns. 1986. Parasitic microfungi on vascular plants in the Yukon and environs. Int. J. Mycol. Lichenol. 2(2-3): 293-347.

Peck, M.E. 1961. *Ericaceae*. *In* A manual of the higher plants of Oregon (2nd edition), P582-596. Binfords & Mort. Publishers.

Peterson, E.B. 1965. Inhibition of black spruce primary roots by a water soluble substance in *Kalmia angustifolia*. For.Sci. 11: 473-479.

Pindell, J. and J.F. Dewey. 1982. Permo-Triassic reconstruction of western Pangea and the evolution of the Gulf of Mexico/Caribbean region. Tectonics 1: 179-211.

Piper, C.V. 1906. *Ericaceae*. *In* Flora of Washington. pp. 436-442. Washington Government Printing Office.

Piper, C.V. and R.K. Beattie. 1915. *Ericaceae*. *In* Flora of the Northwest Coast. pp. 275-283. Press of the New Era Printing Company, Lancaster, PA.

Porsild, A.E. and W.J. Cody. 1980. *Ericaceae*. *In* Vascular Plants Continental Northwest Territories, Canada. pp. 486-497. National Museums of Canada.

Porter, L.J. 1988. Flavans and proanthocyanidins. *In* J.B. Harborne (ed.) The Flavonoids: Advances in research since 1980. pp. 21-62. Chapman and Hall.

Prest, V.K. 1984. The late Wisconsinan glacier complex. *In* R. J. Fulton (ed.), Quaternary stratigraphy of Canada - a Canadian contribution to IGCP project 24. Geological Survey of Canada paper 84 - 10, pp. 21-36, Ottawa.

Preston, R.J., Jr. 1989. North America Trees. 4th ed. Iowa State Univ. Press, Ames.

Pursh, F. 1814. *Kalmia*. *In* Flora Americae Septentrionalis. Vol.I, pp. 295-297. London.

Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. *Ericaceae*. *In* Manual of the Vascular Flora of the Carolinas. pp. 793-817. The Univ. of N.C. Press, Chapel Hill.

Rao, A.S. 1990. Root Flavonoids. Bot. Rev. 56: 1-84.

Rathcke, B.J. 1988a. Interactions for pollination among coflowering shrubs. Ecology 69(2): 446-457.

Rathcke, B.J. 1988b. Flowering phenologies in a shrub community: competition and constraints. J. Ecol. 76: 975-994.

Rathcke, B.J. and L.A. Real. 1993. Autogamy and inbreeding depression in mountain laurel, *Kalmia latifolia* (*Ericaceae*). Amer. J. Bot. 80: 143-146.

Raven, P.H. 1975. The bases of angiosperm phylogeny: cytology. Ann. Missouri Bot. Gard. 62: 724-764.

Raven, P.H. and D.L. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539-673.

Reader, R.J. 1979a. Flower cold hardiness: a potential determinant of the flowering sequence exhibited by bog ericads. Can. J. Bot. 57: 997-999.

Reader, R.J. 1979b. Impact of leaf-feeding insects on three bog ericads. Can. J. Bot. 57: 2107-2112.

Reader, R.J. 1980. Effects of nitrogen fertilizer, shade, and the removal of new growth on longevity of overwintering bog ericad leaves. Can. J. Bot. 58: 1737-1743.

Reader, R.J. 1982a. Geographic variation in the shoot productivity of bog shrubs and some environmental correlates. Can. J. Bot. 60: 340-348.

Reader, R.J. 1982b. Variation in the flowering date of transplanted ericaceous shrubs in relation to their flowering season. J. Biogeog. 9: 397-410.

Reader, R.J. 1983a. Modelling geographic variation in the timing of shoot extension by ericaceous shrubs. Can. J. Bot. 61: 2032-2037.

Reader, R.J. 1983b. Using heatsum models to account for geographic variation in the floral phenology of two ericaceous shrubs. J. Biogeog. 10: 47-64.

Real, L.A. and B.J. Rathcke. 1988. Patterns of individual variability in floral resources. Ecology 69(3): 728-735.

Real, L.A. and B.J. Rathcke. 1991. Individual variation in nectar production and its effect on fitness in *Kalmia latifolia*. Ecology 72(1): 149-155.

Rehder, A. 1932. *Kalmiopsis*, a new genus of *Ericaceae* from Northwest America. Jour. Arn. Arb. 13: 30-34 + a plate.

Rehder, A. 1951. *Ericaceae. In* Manual of Cultivated Trees and Shrubs, Hardy in North America. 2nd edition, revised and enlarged. pp. 691-755. The MacMillan Company, New York.

Riley, J.L. 1984. *Kalmia microphylla* (Hook.) Heller. *In* G.W. Argus, K.M. Pryer, D.J. White, and C.J. Keddy (eds.), Atlas of the Rare Vascular Plants of Ontario. National Museum of Natural Sciences.

Riley, J.L. and S. Walshe. 1985. New and interesting vascular plant records from northern Ontario. Canadian Field-Naturalist 99: 30-33.

Robinson, B.L. and M.L. Fernald. 1908. *Ericaceae In* Gray's New Manual of Botany (7th ed.-illustrated): A Handbook of the Flowering Plants and Ferns of the Central and Northeastern United States and Adjacent Canada. pp. 625-641. American Book Company.

Rohlf, F.J. 1987. NTSYS-pc: Numerical taxonomy and Multivariate Analysis System for the IBM PC. Applied Biostatistics Inc., 3 Heritage Lane, Setauket, NY.

Roig, J.T. and J. Acuña. 1957. *Ericaceae. In* H. Leon and H. Alain. Flora de Cuba. Vol.4, pp. 91-106. Contr. Mus. Hist. Nat. Col. "De La Salle", Habana.

Ruddiman, W.F. and H.E. Wright, Jr. (eds.). 1987. North America and adjacent oceans during the last deglaciation. Boulder, Colorado: Geological Society of America, The Geology of America, v. K-3.

Rydberg, P.A. 1906. *Ericaceae*. *In* Flora of Colorado. pp. 259-260. The Experiment Station, Fort Collins, Colorado.

Rydberg, P.A. 1922. *Kalmia*. *In* Flora of the Rocky Mountains and adjacent plains. 2nd ed., pp. 641-641. New York.

Sakakibara, J., N. Shirai, N. Ishida, and M. Yasue. 1976. Studies on the constituents of the mountain laurel (*Kalmia latifolia* L.). Ann. Rep. Fac. Pharm. Sci. Nagoya City Univ. 24: 31-33. (In Japanese, abstract in English).

Santamour, F.S.,Jr. and R.A. Lucente. 1967. Anthocyanins in the *Ericaceae*. Morris Arboretum Bull. 18: 12-13.

Sargent, C.S. 1890. New or little Known plants. A curious form of *Kalmia*. Garden & Forest 3: 452 (with figure on p. 453).

Sargent, C.S. 1893. *Kalmia In* The Silva of North America. Vol.V, pp. 137-142 (with two plates). Boston and New York: Houghton, Mifflin and Company.

Sargent, C.S. 1922. *Ericaceae*. *In* Manual of the trees of North America. 2nd corrected ed. vol.2, pp. 790-805. Dover Publications, Inc. New York.

Savin, S.M. and R.G. Douglas. 1985. Sea level, climate, and the Central American land bridge. *In* F.G. Stehli and S.D. Webb (eds.), The great American biotic interchange, pp. 303-324, Plenum Publishing Corporation.

Scoggan, H.J. 1979. *Ericaceae*. *In* The Flora of Canada. Part 4, pp. 1194-1213. National Museum of Natural Sciences.

Shaw, R.J. 1989. *Ericaceae*. Vascular Plants of Northern Utah: an Identification Manual. pp. 148-150. Utah State Univ. Press.

Small, E. 1976. Insect pollinators of the Mer Bleue peat bog of Ottawa. Canadian Field-Naturalist 90: 22-28.

Small, J.K. 1903. *Ericaceae*. *In* Flora of the Southeastern United States. pp. 880-890. New York.

Small. J.K. 1914. *Ericaceae*. North Amer. Flora 29: 33-102.

Small. J.K. 1933. *Ericaceae*. *In* Manual of the Southeastern Flora. pp. 991-1006. New York.

Smiley, F.J. 1921. *Ericaceae*. *In* A Report Upon the Boreal Flora of the Sierra Nevada of California. pp. 282-291. Univ. of Calif. Publications in Botany Vol.9, Univ. of Calif. Press, Berkeley, Calif.

Soper, J.H. and M.L. Heimburger. 1982. *Ericaceae*. *In* Shrubs of Ontario. pp. 363-418. ROM.

Southall, R.M. 1973. A Taxonomic Revision of *Kalmia* (*Ericaceae*). Unpublished Ph.D. dissertation, N.C. State Univ., Raleigh.

Southall, R.M. and J.W. Hardin. 1974. A taxonomic revision of *Kalmia* (*Ericaceae*). Jour. Elisha Mitchell Sci. Soc. 90: 1-23.

Southall, R.M. and P.V. Nelson. 1978. The rare white wicky. Am. Nurseryman 148(2): 8, 62-65.

Spethmann, W. 1974. Flavonoide und phenolische inhaltsstoffe in *Rhododendron*-Arten und -Hybriden und ihre möglichen Zusammenhänge zur Chemotaxonomie und Ökologie. Dilomarbeit, Institut fur Angewandte Botanik, Universitat Hamburg: 1-114.

Spethmann, W. 1975. Flavonoide und carotinoide Inhaltsstoffe in *Rhododendron*--Blüten und ihre möglichen Zusammenhänge zur Chemotaxonomie und Farbgebung. *Rhododendron* und immergrüne Laubgehölze, Jahrbuch: 73-99.

Spethmann, W. 1979. Untersuchungen uber das Zustandekommen der Blütenfarbe bei *Rhododendron*. Mitt. Dtsch. Dendrol. Ges. 71: 125-143.

Spethmann, W. 1980. Flavonoids and carotenoids of *Rhododendron* flowers and their significance for the classification of the genus *Rhododendron*. *In* J.L. Luteyn and M.E. O'Brien (eds.), Contributions toward a Classification of *Rhododendron*. pp. 247-275. The New York Botanical Garden.

Spethmann, W. 1987. A new infrageneric classification and phylogenetic trends in the genus *Rhododendron* (*Ericaceae*). Pl. Syst. Evol. 157: 9-31.

Sprague, E. 1781. The *Rhododendron* and "American plants". Little Brown, and Company, Boston.

Stace, C.A. 1989. Plant Taxonomy and Biosystematics (2nd ed.). Edward Arnold.

Stafford, H.A. 1990. Flavonoid Metabolism. CRC Press, Inc. Boca Raton, Florida. 298p.

Stafleu, F.A. and R.S. Cowan. 1988. Wangenheim, Friedrich Adam Julius von. *In* Taxonomic Literature (2nd ed.). Vol. VII: W-Z, p. 56. The Hague/Boston.

Stafleu, F.A. and R.S. Cowan. 1979. Kalm, Pehr. *In* Taxonomic Literature (2nd ed.). Vol. II: H-Le, pp. 487-490. The Hague.

Starling, B.N. 1985. X *Kalmiothamnus ornithomma*. The Plantsman 6: 225-227.

Stebbins, G.L. 1984. Polyploidy and the distribution of the arctic-alpine flora: new evidence and a new approach. Bot. Helvetica 94: 1-13.

Steenis, C.G.G.J. van. 1984. A synopsis of *Alseuosmiaceae* in New Zealand, New Caledonia, Australia and New Guinea. Blumea 29: 387-394.

Stevens, P.F. 1970a. *Calluna*, *Cassiope* and *Harrimanella*: a taxonomic and evolutionary problem. New Phytol. 69: 1133-1150.

Stevens, P.F. 1970b. *Agauria* and *Agarista*: An example of tropical transatlantic affinity. Notes Roy. Bot. Gard. Edinburgh 30: 341-359.

Stevens, P.F. 1971. A classification of the *Ericaceae*: subfamilies and tribes. Bot. J. Linn. Soc. 64: 1-53.

Stone, G.E. 1909. A remarkable form of *Kalmia latifolia*. Rhodora 11: 199-200.

Strand, A.E. and R. Wyatt. 1991. Geographical variation and biosystematics of sand myrtle, *Leiophyllum buxifolium* (*Ericaceae*). Syst. Bot. 16: 529-545.

Stuessy, T.F. 1990. Plant Taxonomy. Columbia Univ. Press, New York. 514p.

Stuessy, T.F. and D.J. Crawford. 1983. Flavonoids and phylogenetic reconstruction. Pl. Syst. Evol. 143: 83-107.

Swain, T. (Ed.). 1963. Chemical Plant Taxonomy. Academic Press, London.

Swain, T. 1976. Nature and properties of flavonoids. *In* T.W. Goodwin (ed.). Chemistry and Biochemistry of Plant Pigments, 2nd edition. Vol.I, pp. 425-463. Academic Press, London, N.Y., and San Francisco.

Swain, T. 1981. Flavonoids as chemotaxonomic markers in plants. *In* F. Czygan (ed.). Pigments in Plants, 2nd Ed. pp. 224-236. Akad.-Verlag: Berlin.

Tămaş, M. 1973. Contributions to the chemotaxonomic study of *Ericales*. III. Flavonoids. St. Cerc. Biochim. 16: 71-81.

Taylor, D.W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and Early Tertiary of the North American area. Bot. Rev. 56: 279-417.

Taylor, R.L. and B. MacBryde. 1978. New taxa and nomenclatural changes with respect to vascular plants of British Columbia: a descriptive resource inventory. Can. J. Bot. 56: 184-195.

Terrell, E.E., S.R. Hill, J.H. Wiersema, and W.E. Rice. 1986. A Checklist of Names for 3,000 Vascular Plants of Economic Importance. 241 p. U.S. Dept. of Agr., Agr. Handbook No. 505.

Thompson, I.D. and A.U. Mallik. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. Can. J. For. Res. 19: 524-526.

Thompson, R.S. 1988. Western North America. *In* B. Huntley and T. Webb III (eds.), Vegetation History, pp. 415-458. Kluwer Academic Publishers.

Thorne, R.F. 1992. Classification and Geography of the Flowering Plants. Bot. Rev. 58: 225-348.

Tidestrom, I. 1925. *Ericaceae*. *In* Flora of Utah and Nevada. pp. 406-408. Washington Government Printing Office.

Tiffney, B.H. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arnold Arbor. 66: 73-79.

Tiffney, B.H. 1985b. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. J. Arnold Arbor. 66: 243-273.

Turner, B.L. and R.E. Alston. 1959. Segregation and recombination of chemical constituents in a hybrid swarm of *Baptisia laevicaulis* x *B. viridis* and their taxonomic implications. Amer. J. Bot. 46: 678-686.

Tutin, T.G., V.H. Heywood, N.A. Burges, D.M.Moore, D.H. Valentine, S.M. Walters and D.A. Webb (editors). 1972. *Ericaceae*. *In* Flora Europaea, Vol.3, pp. 4-18. Cambridge at the University Press.

Wallace, G.D. 1975a. Interrelationships of the subfamilies of *Ericaceae* and derivation of the *Monotropoideae*. Bot. Notiser 128: 286-298.

Wallace, G.D. 1975b. Studies of the *Monotropoideae* (*Ericaceae*) and distribution. The Wasmann J. Biol. 33: 1-88.

Wallace, G.D. 1993. *Ericaceae*. *In* J.C. Hickman (ed.), The Jepson Manual: Higher Plants of California, pp. 544-567, University of California Press, Berkeley.

Wangenheim, F.U.J. 1788. Beschreibung der polenblattrigen *Kalmia* und der gelbbluhenden rosskastanie. Schr. Berlin Ges. Naturf. Freunde 8(3): 129-133.

Warner, B.G. and C.C. Chinnappa. 1986. Taxonomic implications and evolutionary trends in pollen of Canadian *Ericales*. Can. J. Bot. 64: 3113-3126.

Watson, L. 1965. The taxonomic significance of certain anatomical variations among *Ericaceae*. J. Linn. Soc. (Bot.), 59: 111-125.

Watson, L., W.T. Williams, and G.N. Lance. 1967. A mixed-data numerical approach to angiosperm taxonomy: the classification of *Ericales*. Proc. Linn. Soc. Lond., 178: 25-35.

Watson, T.J., Jr. 1977. An analysis of populations formed by hybridization between *Phyllodoce empetriformis* and *P. glanduliflora* (*Ericaceae*). Rhodora 79: 1-16.

Watt, A. 1971. Validation of names of fossil plants described by R.W. Brown in 1962. Taxon 20: 639-641.

Webb, T., III. 1988. Eastern North America. *In* B. Huntley and T. Webb III (eds.), Vegetation History, pp. 385-414. Kluwer Academic Publishers.

Weber, W.A. 1967. *Ericaceae*. *In* Rocky Mountain Flora. pp. 173-177. Univ. of Colorado Press, Boulder.

Welsh, S.L. 1974. *Ericaceae*. *In* Anderson's Flora of Alaska and Adjacent Parts of Canada. pp. 223-237. Brigham Young Univ. Press, Provo, Utah.

Wherry, E.T. 1920. Soil tests of *Ericaceae* and other reaction-sensitive families in northern Vermont and New Hampshire. Rhodora 22: 33-49.

White, D.J. and K.L. Johnson. 1980. The rare vascular plants of Manitoba. Syllogeus 24: 1-57, + maps.

Wilbur, R.L. and C.H. Racine. 1971. The genus *Leiophyllum* (*Ericaceae*): Morphological variation, distribution, and classification. J. Elisha Mitchell Sci. Soc. 87: 222-226.

Williams, A.H. 1964. Dihydrochalcones; their occurrence and use as indicators in chemical plant taxonomy. Nature, 202: 824-825.

Willis, J.C. (Revised by H.K. Airy Shaw). 1966. A dictionary of flowering plants and ferns. 1214p. Cambridge at the University Press.

Wilson, B.F. and J.F. O'Keefe. 1983. Mountain laurel (*Kalmia latifolia* L.) distribution in Massachusetts. Rhodora 85: 115-122.

Wolf, S.J. 1981. A biosystematic revision of *Arnica* L. (Compositae) subgenus *Austromontana* Maguire. Ph.D. dissertation, University of Alberta, Edmonton.

Wolf, S.J. and R. Whitkus. 1987. A numerical analysis of flavonoid variation in *Arnica* subgenus *austromontana* (*Asteraceae*). Amer. J. Bot. 74: 1577-1584.

Wolfe, J.A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madrono 20: 83-110.

Wolfe, J.A. 1972. An interpretation of Alaskan Tertiary Floras. *In* A. Graham (ed.). Floristics and paleofloristics of Asia and eastern North America. pp. 201-233. Elsevier Publishing Company, Amsterdam.

Wolfe, J.A. 1977. Paleogene floras from the Gulf of Alaska region. Prof. Pap. U.S. Geol. Sur. 997.

Wolfe, J.A. 1981. Paleoclimatic significance of the Oligocene and Neogene floras of the Northwestern United States. *In* K.J. Niklas (ed.), Paleobotany, Paleoecology, and Evolution. Vol. 2, pp. 79-101. Praeger, New York.

Wolfe, J.A. 1985. Distribution of major vegetational types during the Tertiary. *In* E.T. Sundquist and W.S. Broecker (eds.). The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. Geophysical Monograph 32: 357-375. American Geophysical Union, Washington, D.C.

Wolfe, J.A. 1987. An overview of the origins of the modern vegetation and flora of the northern Rocky Mountains. Ann. Missouri Bot. Gard. 74: 785-803.

Wollenweber, E. and G. Kohorst. 1981. Epicuticular leaf flavonoids from *Eucalyptus* species and from *Kalmia latifolia*. Z. Naturforsch. 36c: 913-915.

Wollenweber, E. and G. Kohorst. 1984. Novel epicuticular leaf flavonoids from *Kalmia* and *Gaultheria* (*Ericaceae*). Z. Naturforsch. 39c: 710-713.

Wollenweber, E. and M. Jay. 1988. Flavones and flavonols. *In* Harborne, J.B. (ed.). The Flavonoids: Advances in research since 1980. pp. 233-302. Chapman and Hall, London & New York.

Wong, E. 1976. Biosynthesis of Flavonoids. *In* T.W. Goodwin (ed.). Chemistry and Biochemistry of Plant Pigments. 2nd Edition. Vol.I, pp. 464-526. Academic Press, London, N.Y., and San Francisco.

Wood, C.E., Jr. 1961. The genera of *Ericaceae* in the southeastern United States. Jour. Arnold Arb. 42: 10-80.

Wright, H.E., Jr. 1971. Late Quaternary vegetational history of North America. *In* K.K. Turekian (ed.), The Late Cenozoic glacial ages, pp. 425-464, Yale Univ. Press.

Wright, H.E., Jr. 1989. The Quaternary. *In* A.W. Bally and A.R. Palmer (eds.). The Geology of North America - An overview: Boulder, Colorado Geological Soc. of America, The Geology of North America, v. A, pp. 513-536.

Zhilin, S.G. 1989. History of the development of the temperate forest flora in Kazakhstan, U.S.S.R. from the Oligocene to the early Miocene. Bot. Rev. 55: 205-330.

Zika, P.F. and K.T. Dann. 1985. Rare plants on ultramafic soils in Vermont. Rhodora 87: 293-304.

Appendix 1. *Kalmia* Collections Used in the Flavonoid Scan

Notes:

1. A short code is assigned to each population to be used in Appendix 2.
2. All voucher specimens for Part I are deposited at ALTA. Voucher specimens for Part II are indicated by putting the herbarium name in parenthesis at the each entry, without indication, on voucher.
3. In Part II, collections obtained from other institutions are denoted by a star (*), otherwise the material was taken from a herbarium specimen.

I. Collections Made by the Author

Code	Locality	Elev.(feet)	Position
	Kalmia angustifolia		
	var. *angustifolia*		
9107	27.8 km W. of Jctn with Hwy 631 on Hwy 11, Ont.	1200	49°45'N 84°07'W
9109	10 km E. of Mattice on Hwy 11, Ont.	1100	49°38'N 83°07'W
9112	7 km E. of Gregoires Mills on Hwy 11, Ont.	1100	49°18'N 81°50'W
9113	18 km S. of Cochrane on Hwy 11, Ont.	1200	48°57'N 80°57'W
9115	Lac Island Lake camp, Kettle Lakes Prov. Pk., off Hwy 67, Ont.	1300	48°39'N 80°51'W
9116	2 km N. of Jctn with Hwy 66, on Hwy 11, Ont.	1300	48°06'N 80°10'W
9119	18.5 km S. of Jctn with Hwy 391, on Hwy 101, Que.	1250	47°08'N 79°20'W

9120	3 km N. of Temiscaming on Hwy 101, Que.	1200	46°44'N 79°07'W
9123	23 km E. of Matawa, on Hwy 17, Ont.	1100	46°15'N 78°22'W
9124	39.5 km E. of Jctn with Hwy 635 on Hwy 17, Ont.	1000	45°58'N 77°20'W
9125	3 km W. of Jctn with Hwy 241 on Hwy 112, Que.	1020	45°22'N 72°33'W
9126	4 km S. of Black Lake on Hwy 112, Que.	1200	46°01'N 71°21'W
9127	1.4 km S. of Jctn with Hwy 116 on Hwy 20, Que.	600	46°43'N 71°17'W
9129	16 km N. of West Forks on US 201, Me.	1700	45°31'N 70°06'W
9131	1.6 km W. of Jctn with US 202, 9, on Hwy 3, Me.	650	44°27'N 69°33'W
9132	17 km W. of Jctn with Hwy 113, on Hwy 112, N.H.	1500	44°01'N 71°24'W
9133	32 km W. of Jctn with Hwy 113, on Hwy 112, N.H.	2400	44°02'N 71°35'W
9135	Arcadia St. Park, on Hwy 165, 5.6 km E. of Jctn with Woody Hill Rd., R.I.	650	41°45'N 71°41'W
9143	Hartshorne Woods Park, N. of Hwy 36, 1 mile W. of Jctn with Rd. into Sandy Hook Nat'l Pk, N.J.	500	40°24'N 74°00'W
9144	W. side of Rd., ca 7 km S. of Island Beach St. Pk. entrance, N.J.	500	39°42'N 74°09'W
9145	Mile post 72, 10 miles S. of Forked River on US 9, N.J.	500	39°41'N 74°09'W
9148	9.1 km W. of Jctn with US 9 on Hwy 542, N.J.	800	39°39'N 74°10'W
9149	4.9 km N. of Jctn with US 30 on US 206, N.J.	800	39°35'N 74°45'W

9151	1 km N. of Jctn with Hwy 61 on Hwy 42, Penn.	2100	40°49'N 76°20'W

var. *carolina*

9160	0.5 km W. of Jctn with Hwy 677, on Hwy 672, (E. of Whaleyville), VA.	600	36°32'N 76°35'W
9161	Holly Shelter Swamp, N.C.	600	34°35'N 77°54'W
9162	Holly Shelter Swamp, N.C.	600	34°22'N 77°54'W
9163	16 Km N. of Elizabethtown on Hwy 242, N.C.	750	34°45'N 78°36'W
9164	4.7 Km W. of the Jctn with Hwy 242, on White Oak Rd., N.C.	750	34°49'N 78°34'W
9177	Harrison L. Highlands, N.C.	4100	35°03'N 83°11'W
9180	Little Pee Dee St. Pk., N.C.	600	34°20'N 79°17'W
9181	Sand Rd. 0.5 Km E. of Co. Rt. 23, the Jctn of the two is 0.6 Km S. of Hwy 9, S.C.	600	34°11'N 79°08'W

Kalmia cuneata

9165	4.7 Km W. of Jctn with Hwy 242, on White Oak Rd., N.C.	750	34°49'N 78°34'W

Kalmia hirsuta

9182	2.3 Km W. of Jctn with I-95, on Hwy 68, S.C.	550	32°42'N 80°52'W
9183	3.4 Km E. of Jctn with US 601, on Hwy 652, S.C.	600	32°36'N 81°08'W
9184	6.5 Km W. of Jctn with I-95, on Hwy 204, GA.	600	32°03'N 81°12'W

9185	1.5 Km N. of Jctn with Hwy 46, on Hwys US 1 & GA 4, 1.5 Km S. of I-16, GA.	600	32°24'N 82°18'W
9186	10.7 Km S. of Jctn with Hwy 147, on US 1, GA.	800	31°51'N 82°21'W
9187	4.7 Km E. of Jctn with US 1, on US 341 & GA 27, GA.	600	31°47'N 82°19'W
9188	13.5 Km S.E. of Jctn with US 301, on US 341, 25 & GA 27, GA.	600	31°33'N 81°49'W
9189	0.5 Km S. of the Crooked R. St. Pk. entrance, on Hwy 40 (Spur), GA.	550	30°50'N 81°32'W
9190	10.9 Km S.of Jctn with US 1, 23 & 301, on Hwy 121, GA.	450	30°47'N 82°02'W
9191	0.5 Km S. of Jctn with Hwy 94, on Co. Rt. 121 and 119, N.W. of Bryceville, FL.	450	30°30'N 81°56'W
9192	1.2 Km W. of Jctn with Hwy 19, on Hwy 20, SW. of Palatka, FL.	500	29°37'N 81°39'W
9193	7.2 Km S. of Jctn with Hwy 20, on Hwy 315, S. of Interlachen, FL.	500	29°33'N 81°57'W
9194	Roadside opposite the Bens Hitching Post Campground, ca. 5 Km E. of Jctn with Hwy 315, on Hwy 40, FL.	550	29°12'N 81°55'W
9195	0.3 Km E. of Jctn with Hwy 19, on Hwy 445 (Lake Co. Rt.), FL.	350	29°09'N 81°32'W
9196	3.5 Km NE of Jctn with US 129, on Hwy 47 (near Trenton), FL.	400	29°38'N 82°50'W
9198	10.4 Km E. of Jctn with Hwy 12 (Bristol), on Hwy 20, FL.	600	30°24'N 84°56'W
9199	3.8 Km N. of Jctn with US 98 (Carrabella), on Hwy 67, Fl.	400	29°52'N 84°40'W
91100	13.5 Km W. of Jctn with US 98, on Hwy 30E, Gulf Co. Fl.	400	29°40'N 85°24'W

91101	5.2 Km. W. of Jctn with Hwy 30, on Hwy 30E, St. Joseph Peninsula, FL.	400	29°40'N	85°27'W
91102	St. Andrews St. Pk., Panama City, FL.	400	30°08'N	85°48'W
91103	14.9 Km W. of Jctn with Hwy 79, on US 98, FL.	400	30°17'N	86°02'W
91104	22.1 Km W. of Jctn with US 331, on US 98, FL.	400	30°20'N	86°27'W
91105	25 Km W. of Jctn with Hwy 87, on US 98, FL.	400	30°22'N	87°11'W
91106	2 Km W. of Jctn with Hwy 161, on Hwy 180 (NW corner btwn Hwy 180 & Gulf Bay Rd.), AL.	400	30°16'N	87°42'W
91107	3.4 Km S. of Munson Elementary School, on Hwy 191, Blackwater R. State Forest, FL.	600	30°48'N	86°58'W

Kalmia latifolia

9136	Arcadia St. Pk, 5.6 Km E. of Jctn with Woody Hill Rd., R.I.	650	41°45'N	71°41'W
9137	At Jctn of Hwy 2 & Marlborugh Business Rd. (W. branch), CT.	800	41°42'N	72°28'W
9138	Marlborugh, CT.	800	41°35'N	72°30'W
9139	5.4 Km N. of jctn with Hwy 82, on Hwy 11, CT.	820	41°28'N	72°17'W
9140	Mt. Arlington, E. side of Lake Lakawanna, N.J.	1500	40°58'N	74°40'W
9141	Cliffwood. at the back of a school, N.J.	600	40°29'N	74°19'W
9142	Harrshorne Woods Pk., W. of Sandy Hook Nat'l Pk., N.J.	500	40°24'N	74°00'W
9146	Mile post 72, 10 mi. S. of Forked R., on US 9, N.J.	500	39°41'N	74°09'W

9147	Baker's Acres Campground, Parkertown, N.J.	500	39°40'N	74°08'W
9150	0.6 Km W. of Jctn with Hwy 419, on Hwy 183, Penn.	1800	40°29'N	76°11'W
9152	1 Km N. of Jctn with Hwy 61, on Hwy 42, Penn.	2100	40°49'N	76°20'W
9153	2.6 Km W. of Trevorton, on Hwy 225, Penn.	1400	40°46'N	76°41'W
9154	Pine Grove Furnace St. Pk., on Hwy 233, Penn.	1400	40°01'N	77°16'W
9155	5.5 Km E. of Jctn with Hwy 977, on Hwy 233, Penn.	2000	39°50'N	77°32'W
9156	2 Km N. of Jctn with Hwy 234, on US 301, MD.	750	38°26'N	76°57'W
9157	1.9 Km S. of Jctn with US 33, on Skyline Drive, VA.	3100	38°23'N	78°31'W
9158	34 Km N. of Jctn with US 250, on Skyline Drive, VA.	2800	38°14'N	78°43'W
9159	Colonial Nat'l Hist. Pk., Newport News, VA.	600	37°14'N	76°31'W
9166	2.7 Km N. of Jctn with US 19E, on Buck Mt.Rd., Tenn.	3400	36°11'N	82°03'W
9167	5 Km N.W. of Jctn with US 19E, on Hwy 226, N.C.	2900	35°56'N	82°05'W
9168	5.4 Km S. of Jctn with Hwy 226, on Blue Ridge Pkwy, N.C.	3900	35°51'N	82°05'W
9169	7.4 Km S. of Jctn with I-40, on Hwy 9, N.C.	3000	35°35'N	82°18'W
9170	Echo Lakes, Hendersonville, N.C.	2600	35°19'N	82°28'W
9171	18.7 Km W. of Jctn with Hwys 191 & 280, on N. Mills R. forest Rd., Pisgah Nat'l Forest, N.C.	3200	35°25'N	82°40'W
9172	23.1 Km S. of Jctn with Hwy 191, on Blue Ridge Pkwy, N.C.	5000	35°24'N	82°45'W

9173	31.2 Km S. of Jctn with Hwy 276, on Blue Ridge Pkwy (highest point), N.C.	6000	35°27'N 82°08'W
9174	3.2 Km E. of Jctn with US 321, on Foothill Pkwy, Great Smoky Mtns., Tenn.	1900	35°42'N 83°50'W
9175	21.3 Km E. of Jctn with US 129, on Hwy 28, N.C.	2600	35°24'N 83°43'W
9176	3.5 Km N. of Highlands, on Hwys 28 & US 64, bank of Little Tenn. R., N.C.	3500	35°04'N 83°43'W
9178	11.3 Km S.E. of Clayton, on Hwys 28 & US 76, GA.	1800	34°48'N 83°17'W
9179	ca. 12 mi. N. W. of Walhalla, on Hwy 28, S.C.	2800	34°51'N 83°08'W
9197	Glen Julia Pk, Mt. Pleasant, FL.	700	30°38'N 84°42'W

Kalmia microphylla

AB-001	Bog btwn Cardinal Divide and Fairfax L. Alta.	4000	52°54'N 117°07'W
AB-002	Fairfax L. Alta.	3800	52°58'N 116°35'W
AB-003	7.5 Kms S. of Cardinal R. on Forest Rd. to Nordeg, Alta.	3500	52°49'N 116°25'W
AB-005	Cameron L., Waterton Lakes Nat'l Pk, Alta.	5500	49°02'N 114°03'W
AB-006	Summit Lake, Waterton Lakes Nat'l Pk, Alta.	6200	49°01'N 114°02'W
BC-001	Kusawak L. Haines Hwy. B.C.	3300	59°42'N 136°36'W
BC-002	Bog 24 Kms S. of Disease L. on Cassier Hwy, B.C.	4200	58°11'N 129°52'W
BC-003	McBbride peak, B.C.	6065	53°20'N 120°08'W
BC-004	Lower Elk L. Prov. Pk, B.C.	5550	50°34'N 115°07'W

BC-005	25 Kms S. of Elk Prov. Pk, along Forest Rd., B.C.	5400	50°22'N	114°55'W
BC-006	Bridal L. on Hwy 3 (the Pass btwn Creston and Salmo), B.C.	5800	49°05'N	117°02'W
BC-007	1 Km W. of Trout L. (Post) on Hwy 31, B.C.	2500	50°39'N	117°33'W
BC-008	Btwn No.4 & No.5 Rd., N. of Westminster Hwy, Richmond, B.C.	100	49°10'N	123°07'W
BC-009	First L., Cypress Prov. Pk, B.C.	3200	49°23'N	123°11'W
YT-001	MacMillan Pass, N.W.T.	4200	63°16'N	130°56'W
YT-002	S. of MacMillan R., Bridge #2, 208 Kms from Ross R. on N. Canol Rd. Yukon	3600	63°12'N	130°57'W
9001	Near Inverness River. S.W. of S.W. of Shell Plant, Swan Hills, Alta	3100	54°56'N	115°41'W
9002	Pine Point, N.W.T.	820	60°41'N	114°28'W
9003	11 Kms S.W. of Pine Point on Hwy 6, N.W.T.	840	60°41'N	114°52'W
9043	8 Kms E. of Port Renfrew, on Hwy 14, V.I., B.C.	600	48°31'N	124°21'W
9044	6 Kms N. of Jctn with Hwy 4, on Ucluelet-Tofino Rd., V.I., B.C.	200	49°02'N	125°38'W
9045	3 Kms S. of Tofino, on Ucluelet-Tofino Rd., V.I., B.C.	150	49°08'N	125°53'W
9046	4 Kms E. of Ucluelet-Tofino Rd., on Hwy 4, V.I., B.C.	120	49°02'N	125°33'W
9047	22 Kms E. of Ucluelet-Tofino Rd., on Hwy 4,	150	49°05'N	125°22'W
9048	No name L. S. of Hwy 19 at Jctn with the Rd. to Schoen L., V.I., B.C.	900	50°12'N	126°27'W

9049	3 Kms E. of Port McNeil Rd. on Hwy 19, V.I., B.C.	200	50°33'N	127°01'W
9050	Corner at Jctn btwn Hwy 19 & S. branch Rd. to Port Hardy Airport, V.I., B.C.	200	50°41'N	127°24'W
9051	S.E. corner at Jctn btwn Hwy 19 & the Rd to Port McNeil, V.I., B.C.	400	50°33'N	127°06'W
9052	24 Kms W. of Sayward Jctn on Hwy 19, V.I., B.C.	920	50°21'N	126°05'W
9053	48 Kms N. of Campbell R., on Hwy 19, V.I., B.C.	500	50°15'N	125°40'W
9054-7	Four Small Lakes along Bunch Berry Trail, on Forbidden Plateau, V.I., B.C.	3100	49°38'N	125°13'W
9058	8.2 mi E. of Granite Falls, on Hwy 92, Wash.	900	48°06'N	121°52'W
9059	9 kms N. of Humptulips, on Hwy 101, Wash.	500	47°19'N	123°55'W
9060	Siesta L. Yosemite Nat'l Pk, Calif.	7600	37°51'N	119°40'W
9061	Small L., 1 Km E. of May L. campground Rd. on Tioga Rd., Yosemite Nat'l Pk., Calif.	8080	37°47'N	119°29'W
9062	Emerald L. Lassen Nat'l Pk Calif.	7900	40°28'N	121°31'W
9063	Upper Meadow, Lassen Nat'l Pk., Calif.	7400	40°28'N	121°28'W
9064	Meadow, 1 Km. E. of Cove L. 11 Kms from Hwy 395, on Modoc County Rd 2, Calif.	7400	41°59'N	120°12'W
9065	1 Km below Lamoille L., Ruby Mtn Scenic Area, Nevada.	9000	40°36'N	115°23'W
9066	Meadow below Boulder Lakes, Sawtooth Nat'l Recreation Area, Idaho.	9000	43°51'N	114°30'W

9067	Jctn btwn Island L. Rd & Hwy 212, Wyoming.	9100	44°57'N 109°32'W
9068	A small L. 16 Kms S.W. of Wyoming & Montana Boarder, Hwy 212, Wyoming.	9500	44°57'N 109°30'W
9069	Meadow above the Long L. on Hwy 212, Wyoming.	10000	44°58'N 109°29'W
9070	Blue L. below the Crazy Peak, Crazy Mtns., Montana.	8100	46°02'N 110°17'W
9071	Meadow Below the Logan Pass, Glacier Nat'l Pk, Montana.	6500	48°42'N 113°40'W
9201	Roadside, 49 Kms S. of Jctn btwn Hwy 40 & Musreau L., Alta.	4500	54°08'N 118°58'W

Kalmia polifolia

AB-001	Anzac, Alta.	1800	56°27'N 111°02'W
AB-002	Bog ca. 20 Kms from Ft. Mckay, east of Athabasca R., Alta.	1500	57°17'N 117°38'W
AB-003	A small L. 5 Kms N. of Cottonwood Creek, Hwy 881, Alta.	1800	56°08'N 119°55'W
AB-004	Bog & disturbed area, 0.2 Kms N. of Gregorie R., Hwy 881, Alta.	1950	57°22'N 111°00'W
AB-005	43 Kms N. of Mariana L. on Hwy 63, Alta.	2300	56°12'N 111°45'W
AB-006	Ca. 40 Kms S. of Mariana L., 2 Kms N. of House R. on Hwy 63, Alta.	2300	55°42'N 112°10'W
9004	27 Kms S.W. of Jctn with Hwy 903, on Hwy 904, Sask.	2200	54°45'N 108°28'W
9005	At N.E. corner of Jctn btwn Hwy 965 & Canoe L. Rd. Sask.	1800	55°08'N 108°09'W
9006	ca. 35 Km W. of Jctn with Hwy 155, on Hwy 965, Sask.	1800	55°09'N 108°07'W

9007	43 Kms N. of Jctn with Hwy 965, on Hwy 155, Sask.	1700	55°29'N 108°05'W
9008	17 Kms S.of Buffalo Narrows, on Hwy 155, Sask.	1600	55°43'N 108°22'W
9009	18 Kms N. of Buffalo Narrows, on Hwy 155, Sask.	1600	56°02'N 108°38'W
9010	Lac la Plonge Campground, 1.2 Kms off Hwy 165, Sask.	1700	55°10'N 107°30'W
9011	54 Kms E. of Jctn with Hwy 155, on Hwy 165, Sask.	1600	55°12'N 106°52'W
9012	0.5 Kms E. of Smoothstone R. on Hwy 165, Sask.	1600	55°09'N 106°12'W
9013	4 Kms N. of (S)Jctn with Hwy 165, on Hwy 2, Sask.	1500	54°42'N 105°41'W
9014	ca. 7 Kms S.W. of Missinipe on Hwy 2, Sask.	1300	55°34'N 104°50'W
9015	32 Kms N. of McLennana L. on Hwy 102, Sask.	1300	56°05'N 103°53'W
9016	28 Kms E. of (N)Jctn with Hwy 2 on Hwy 165, Sask.	1100	54°43'N 105°01'W
9017	9 Kms E. of Jctn with Hwy 165 (W. branch), on Hwy 106, Sask.	900	54°31'N 104°07'W
9018	1.1 Kms E. of Jctn with Hwy 911, on Hwy 106, Sask.	800	54°41'N 103°17'W
9019	36 Kms E. of Jctn with Hwy 135, on Hwy 106, Sask.	900	54°40'N 102°18'W
9020	4 Kms E. of Jctn with Hwy 392, on Hwy 39, Man.	800	54°38'N 99°52'W
9021	7 Kms W. of Ponton, on Hwy 39, Man.	700	54°38'N 99°13'W
9023	0.5 Kms E.of Jctn with Hwy 6, on Hwy 375, W. of of Paint L. Man.	700	55°32'N 98°04'W
9024	13 Kms W. of Jctn with the Rd. to Split L. on Hwy 280, Man.	700	56°18'N 95°58'W

9025	24 Kms E. of Split L. Rd., on Hwy 280, Man.	700	56°22'N 95°40'W
9026	89 Kms E. of Split L. Rd., on Hwy 280, Man.	700	56°25'N 95°05'W
9027	At the Jctn btwn Hwys 280 & 290, 30 Kms N. of Gillam, Man.	600	56°26'N 94°33'W
9028	Chesnaye, Man.	400	58°12'N 94°09'W
9029	1.5 mi N. of Chesnaye, Man.	400	58°13'N 94°09'W
9030	2.5 mi N. of Chesnaye, Man.	400	58°14'N 94°09'W
9031	4.5 mi N. of Chesnaye, Man.	380	58°16'N 94°09'W
9032	Lamprey, Man.	380	58°19'N 94°09'W
9033	4 mi N. of Lamprey, Man.	380	58°23'N 94°08'W
9034	Bylot, Man.	350	58°26'N 94°08'W
9035	Digges, Man.	280	58°32'N 94°08'W
9036	1.5 mi S. of Tidal, Man.	260	58°39'N 94°08'W
9037	77 Kms S. of Ponton, on Hwy 6, Man.	700	54°06'N 99°11'W
9038	8 Kms N. of Grand Raphids, on Hwy 6, Man.	700	53°12'N 99°20'W
9039	37.5 Kms W. of Jctn with Hwy 327, on Hwy 60, Man.	800	53°05'N 100°12'W
9040	N.E. Corner at Jctn btwn Hwys 10 & 60, Man.	800	53°19'N 101°08'W
9041	1 Km E. of Hudson Bay, on Hwy 3, Sask.	1100	52°52'N 102°21'W
9042	8 Kms S.E. of Crooked River, on Hwy 23, Sask.	1400	52°43'N 103°41'W
9101	17 km E. of Jctn with Hwy 307 on Hwy 44, Man.	1400	49°48'N 95°18'W
9102	12 km E. of Jctn with Hwy 71 on Hwy 17, Ont.	1600	49°45'N 94°05'W

9103	2.3 km E. of Jctn with Hwy 622 on Hwy 17, Ont.	1800	49°31'N 92°05'W
9104	11.9 km E. of English River on Hwy 17, Ont.	1830	49°13'N 90°50'W
9105	20.2 km N. of Jctn with Hwy 17 on Hwy 11, Ont.	1080	49°12'N 88°12'W
9106	25.8 km E. of Jctn with Hwy 801 on Hwy 11, Ont.	1300	49°42'N 87°21'W
9108	27.8 km W. of Jctn with Hwy 631 on Hwy 11, Ont.	1200	49°45'N 84°07'W
9110	10 km E. of Mattice on Hwy 11, Ont.	1100	49°38'N 83°07'W
9111	7 km E. of Gregoires Mills on Hwy 11, Ont.	1100	49°18'N 81°50'W
9114	18 km S. of Cochrane on Hwy 11, Ont.	1200	48°57'N 80°57'W
9117	2 km N. of Jctn with Hwy 66 on Hwy 11, Ont.	1300	48°06'N 80°10'W
9118	18.5 km S. of Jctn with Hwy 391, on Hwy 101, Que.	1250	47°08'N 79°20'W
9121	3 km N. of Temiscaming on Hwy 101, Que.	1200	46°44'N 79°07'W
9122	23 km E. of Matawa, on Hwy 17, Ont.	1100	46°15'N 78°22'W
9128	26 km N. of West Forks on US 201, ME.	1900	45°33'N 70°07'W
9130	16 km N. of West Forks on Us 201, Me.	1700	45°31'N 70°06'W
9134	32 km W. of Jctn with Hwy 113 on Hwy 112, N.H.	2400	44°02'N 71°35'W
9202	Maqua L. end of Stony Mt. Rd. off Hwy 63, Alta.	2300	56°21'N 111°18'W

II. Collections Made by Others

Code	Collector & #	Locality
	Kalmia angustifolia	
	var. *angustifolia*	
AW*	Alex Wilson	Peggy's Cove, Halifax Co., N.S
JKM*	J.K. Morton	French R. Hwy 69, Ont. (ALTA)
New-3*	R.E. Newell	Mud Lake, King Co. N.S. 44°75'N 64°25'W. (ALTA)
New-4*	R.E. Newell	Aylesford Sand Barrens, Kings Co. N.S. 45°10'N 64°55'W. (ALTA)
PJS*	P.J. Scott	1 Km along Mt. Scio Rd from Jctn with Groves Rd. St. John's, Nfld. (ALTA)
	Var. *carolina*	
Dismal	E.J. Grimes #4517	Portsmouth Ditch, 5 mi from L. Drummond, Dismal Swamp, VA. (NY)
Dixon	H.N. Moldenke #1242	Near Dixon, Onslow Co. N.C. (NY)
Edisto	S.G. Sayer	Edisto Island, S.C. (NY)
Flat	E.J. Alexander T.H. Everett S.D.Pearson	Flat Rock, N.C. (NY)
Jack	?	Jackson Co., N.C. (ALTA)
Mann	T.F. Daniel #17	3 mi W. of Mann's Harbor on U.S. 64, N.C. (NY)
Roslin	H.E. Ahles #29805	2.4 mi S. of Roslin, Cumberland Co. N.C. (DAO)

Shady	A.J. Sharp #1552 J.K. Underwood	Shady Valley, near Mountain City Johnson Co. Tenn. (NY)

Kalmia cuneata

Bladen	?	Bladen Co. N.C. (ALTA)
Harts	B.E. Smith	Bay near Golf Course, Hartsville, S.C. (NY)
Holly	J. Mcmenamin	Holly Refuge Swamp, Pender Co. N.C. (NY)
Pine	R.E. Wicker	Pinehurst, N.S. (NY)

Kalmia ericoides

var. *aggregata*

VA1	E.L. Ekman	Santa Barbara, Isle of Pines, Cuba. (NY)
VA2	E.L. Ekman	Loma Dagville, Isle of Pines, Cuba. (NY)
VA3	E.P. Killip #42882	Los Indios, Sabanas, Isle of Pines, Cuba. (NY)
VA4	N.L. Britton #14146 E.G. Britton P. Wilson	San Pedro and vicinity, Isle of Pines, Cuba. (NY)
VA5	Marie-Victorin Alain #77	Sables blancs de Los Indios, Isle of Pines, Cuba. (NY)
VA6	E.P. Killip #43001	Sabanas along Rd to Playa, Playa Roja, Bahia de Siguanea, Cuba. (NY)

var. *ericoides*

VE1	E.L. Ekman	Arroyo Mantua, Piñar del Rio, Cuba. (NY)
VE2	E.L. Ekman	Piñar del Rio, Cuba. (NY)

VE3	E.L. Ekman	Laguua Larga, Larifa, Piñar del Rio, Cuba. (NY)

Kalmia latifolia

NB784*	G. Newberry #10784	Spartanbury Co. S.C. (ALTA)
NB802*	G. Newberry #10802	Cherokee Co. S.C. (ALTA)
NB809*	G. Newberry #10809	Kings Cr. Cherokee Co. S.C. (ALTA)
NB819*	G. Newberry #10819	Kings Mt.State Pk. York Co. S.C. (ALTA)
NB861*	G. Newberry #10861	Greenville Co. S.C. (ALTA)
NS313*	J.B. Nelson #9313	Aiken Co. S.C. (ALTA USCH)
NS336*	J.B. Nelson #9336	Vaucluse, Aiken Co. S.C. (ALTA USCH)
NS590*	J.B. Nelson #9590	Pickens Co. S.C. (ALTA USCH)

Kalmia microphylla

A13882	E.H. Moss #4720	Cavell Glacier, Jasper Nat'l Pk. Alta. (ALTA)
A30296	A.E.&R.T. Porsild #3509	Etach Point, Great Bear L. N.W.T. 66°00'N 121°30'W. (ALTA)
A57455	I. Corns	Musreau L. Alta 54°08'N 118°37'W. (ALTA)
A78645	R.E.Reid #425	Norman Wells, N.W.T. 65°38'N 94°31'W. (ALTA)
A78967	Zool students	Wood Buffalo Nat'l Pk, Alta. 59°30'N 114°50'W. (ALTA)
A79405	N.G. Kondla #2028	Kananaskis Prov. Pk., Alta 50°41'N 115°09'W. (ALTA)
C88255	A.E. Porsild #5595	Lake on Tha-anne R. Keewatin District, N.W.T. 60°58'N 97°00'W. (CAN)

C252181	W.O. Pruitt Jr. #21	Beverley L. N.W.T. 64°43'N 100°15'W. (CAN)
C342230	J.H. Scoper #12926 M.J. schepanek	Mt.Revelstoke Nat'l Pk, B.C., Elev. 6000', 51°02'N 118°09'W. (CAN)
D135252	R. Hainault #7550	Scout L., Cathedral Pk., B.C. Elev. 7550. (DAO)
D169629	L. Ovenden J.S. Rowe	Eastern Great Slave L. Region, N.W.T. (DAO)
D401923	W.J. Cody #33128 J.H. Ginns	Ogilvie & Wernecke Mtns, Yukon. (DAO)
D473045	J.P. Anderson #6338	Juneau, Alaska. (DAO)
D473147	W.J. Cody #1832	Churchill, Man. 57°45'N 94°05'W. (DAO)
D473183	R.L. Taylor #3	10 mi SSE of Juskatla, Graham Is. Q.C.I., B.C. (DAO)
D473192	J.A. Calder #21996 D.B.O. Savile R.L. Taylor	Moresby Is. Q.C.I., B.C. (DAO)
D473234	R. Pillsbury #285	Prince Rupert, B.C. (DAO)
D473309	J.A. Calder K.T. MacKay	Elk R. Valley, Strathcona Prov. Pk.,V.I., B.C. 49°46'N 125°51'W. (DAO)
D473315	J.A. Calder #32473 K.T. MacKay	W. end of Burman L. below the Golden Hinde, V.I., B.C. Elev. 3900', 49°39'N 125°51'W. (DAO)
D473328	L.R.J. Dennis #2274	Ridge N. of Jefferson Pk, Marion Co. Oregon. Elev. 6500'. (DAO)
JWT708	J.W. Thompson #9708	Snoqualmie Pass, King Co. WA. Elev. 3000'. (NY)
NY-BG	H.H. Bartlett #791	Clackamas L. Clackamas Co. Oregon. (NY)

Kalmia polifolia

AW*	Alex Wilson	Peggy's Cove, Halifax Co. N.S. (ALTA)
NW-1*	R.E. Newell	Mud Lake, Kings Co., N.S. (ALTA)
NW-2*	R.E. Newell	Aylesford Sand Barrens, Kings Co. N.S. (ALTA)
PJS*	P.J. Scott	1 Km along Mt. Scio Rd from Jctn with Groves Rd, St.John's, Nfld.

Appendix 2. Flavonoid Distribution Matrix in *Kalmia*

Notes:

1. The heading of each population is the same as the code provided in Appendix 1.
2. The flavonoid order in the matrices follows the Table at the end of this Appendix, with 1&2 combined as 1.
3. Numbers in the matrices are assigned according to the flavonoid spot concentration on the 2D paper chromatograms: 0 = not detectable; 1 = detectable; 3 = highly concentrated; 2 = concentration falling between 1 and 3.

I. *Kalmia angustifolia*

Var.*angustifolia*								
9107	2010000013	0001310010	0010000020	0000000000	0010000032	1000000100	0300000330	02220
9109	0020000013	0001310110	0000000020	0000000000	0010000021	1000000100	0300000030	03110
9112	2020000013	0001320210	0000001020	0000000000	0010000031	2010000100	0300000231	02220
9113	2220000013	0001310210	0010002020	0000000000	0010000031	3000000100	0300000230	02320
9115	3000000013	0001210210	0000003020	0000000000	0000000031	2010000100	0300000230	02110
9116	3010000013	0002210110	0000002020	0000000000	0010000031	2010000100	0300000031	02110
9119	2020000013	0002330310	0000003020	0000000000	0010010031	2120000100	0300000320	03220
9120	2020000013	0002320200	0110002020	0000000000	0010000030	2120000100	0300000322	02220
9123	1220000013	0001320200	0000002010	0000000000	0010000031	2120000100	0300000321	02110
9124	1020000013	0002320320	0010001030	0000000000	0010000030	2120000100	0300000230	02120
9125	2120000013	0002320210	0110002020	0000000000	0010020130	2120000100	0300000322	02120
9126	3020000013	0003220210	0000002020	0000000000	0020020030	3120000100	0300000032	03020
9127	3030000013	0002320210	0000002020	0000000000	0020020030	3120000100	0300000232	03020
9129	2020000013	0002320310	0020002020	0000000000	0010020031	3010000100	0300000332	03130
9131	3220000013	0002320110	0000002020	0000000000	0010020030	3020000100	0300000231	03320
9132	3020000013	0002320110	0000002010	0000000000	0010020030	3020000100	0300000331	03220
9133	2120000013	0002310310	0000002020	0000000000	0010020031	3010000100	0300000332	03220
9135	2220000013	0001320110	0000002020	0000000000	0010010031	3120000000	0300000122	03230
9143	2210000013	0001320210	0000001000	0000000000	0010023031	3020000100	0200000321	03110
9144	2010000013	0001320310	0000003020	0000000000	0010010031	3020000100	0200000322	03110
9145	2010000013	0002320310	0000002000	0000000000	0010010031	3020000100	0200000322	03000
9148	2010000023	0002320310	0120002000	0000000000	0010010031	3020000100	0200000322	03220
9149	2110000023	0002320310	0120002000	0000000000	0010020031	3020000100	0300000333	03220
9151	1210000023	0002320320	0220002000	0000000000	0010010031	3120000100	0200000323	03110
AW	2000000013	0001200200	0000002010	0000000000	0020000010	1010000100	0300000231	00110
JKM	3000000023	0001200100	0010001000	0000000000	0000000000	0000000100	0300000320	00120
NEW3	2000000023	0001300200	0010000000	0000000000	0000000000	0000000000	0300000320	00210
NEW4	3000000013	0002300110	0000000010	0000000000	0000000010	1000000100	0300000230	02210
PJS	3000000013	0001300010	0000000020	0000000000	0000000010	1000000100	0300000220	00120
Var. *carolina*								
9160	0000000013	0003310210	0330002010	0000000000	0010000000	0000000000	0300000223	00230
9161	0110000013	0002300210	0330002020	0000000000	1010000003	0000000000	0300000202	02330
9162	0000000013	0002320110	0030001030	0000000000	0010000003	0000000000	0300000003	01330
9163	0000000013	0001310110	0030001030	0000000000	0010000023	0000000000	0300000003	01330
9164	0000000013	0001310110	0130002010	0000000000	0010000000	0000000000	0300000003	00332
9177	0010000013	0001320310	0130002000	0000000000	0020000002	2000000000	0300000203	02122
9180	0000000013	0001320120	0130001030	0000000000	0020000002	2000000000	0300000003	01322
9181	0000000013	0001320220	0230002010	0000000000	0020000002	2000000000	0300000203	02322
DISMAL	0000000023	0001210110	0030000020	0000000000	0020000002	2000000000	0300000013	01220
DIXON	2000000023	0001200120	0020000020	0000000000	0020000020	0000000000	0200000003	00220
EDISTO	0000000023	0002300210	0030000020	0000000000	0020000022	2000000000	0200000003	02030
FLAT	0000000013	0002330210	0230002030	0000000000	0020000022	2000000000	0100000003	01320
JACK	0000000023	0002320310	0000000020	0000000000	0010000032	3000000100	0200000003	01020
MANN	0010000013	0001310110	0130001010	0000000000	2020000012	2000000000	0200000003	02220
ROSLIN	2000000013	0002320110	0230001000	0000000000	2020000022	2000000100	0100000003	02220
SHADY	0000000023	0002320310	0220002000	0000000000	0020000022	2000000100	0200000003	01020

II. *Kalmia cuneata*

9165	0010010133	0001330311	0010000000	0000000000	0010100000	0000100100	0100000000	01000
BLADEN	0000010223	0002330311	0020000000	0000000000	0010100000	0000000000	0100000000	02000
HARTS	0000110233	0001130311	0010000000	0000000000	0000000000	0000000000	0100000000	02000
HOLLY	0010000133	0003330311	0010000000	0000000000	0000100000	0000000000	0200000000	02000
PINE	0010010023	0001120311	0000000000	0000000000	0000000000	0000000100	0100000000	03000

III. *Kalmia ericoides*

Var. *aggregata*								
VA1	3000000023	0003100110	0000000000	0000000000	0000100000	0000000000	0200000002	03001
VA2	3000000033	1003300323	0000000000	0000000000	0000100000	0000000000	0300000002	00003
VA3	3000010023	1003110310	0000000020	0000000000	0000100000	0000000000	0200000201	00001
VA4	3000001233	1003300310	0000000000	0000000000	0000100000	0000000000	0300000302	01002
VA5	3000001233	2003300320	0000000020	0000000000	0000200000	0000000000	0100000302	00000
VA6	3200001133	0003300322	0000000000	0000000000	0000100000	0000000000	0200000202	01002
Var. *ericoides*								
VE1	2030021033	0000300320	0000002010	0000000000	0000100000	0000000000	0200000202	02003
VE2	3030022333	2000300310	0000000020	0000000000	0000100000	0000000000	0100000001	01002
VE3	3130033323	2000300310	0000000010	0000000000	0000100000	0000000000	0300000002	02002

IV. *Kalmia hirsuta*

9182	3020011022	0000200320	1000003000	0101000000	0000100000	0000000100	0200000002	01000
9183	3010011022	0000200311	1000003000	0101100000	0000000000	0000000100	0200000002	02000
9184	3020011023	0000200310	1000002000	0101100000	0000000000	0000000100	0200000001	03000
9185	3020011032	0000200310	1000002000	0203200000	0000100000	0000100100	0100000002	02000
9186	3020011022	0000200310	1000002000	2203200000	0000000000	0000100100	0100000001	02000
9187	3020011022	0000200310	1000002000	2203200000	0000000000	0000100100	0100000001	02000
9188	3120011022	0000200310	1000002000	1301200000	0000000000	0000100100	0200000001	02000
9189	3020022023	0000300310	1000002000	0201100000	0000000000	0000000100	0200000001	02000
9190	3020011033	0000300310	1000003000	0001000000	0000000000	0000000100	0200000002	02000
9191	3030011033	0000320310	1000003000	1202200000	0000000000	0000000100	0100000001	02000
9192	3030011033	0000300310	1000003000	0001000000	0000000000	0000000100	0200000001	02000
9193	3030011033	0000300310	1000003000	0101000000	0000000000	0000000100	0200000002	02000
9194	3020011023	0000300310	1000003000	0101100000	0000000000	0000000100	0200000001	02000
9195	3030011023	0000300310	1000003000	0201200000	0000000000	0000000100	0200000001	02000
9196	3030011033	0000300310	1000003000	0001200000	0000000000	0000100100	0200000001	02000
9198	3030112033	0000300310	1000003000	0001200000	0000000000	0000000100	0200000002	02000
9199	3020011023	0000300310	1000002000	0001100000	0000000000	0000000100	0300000002	02000
91100	3030012023	0000300311	1000003010	2303300000	0000100000	0000000100	0200000002	03000
91101	3030011033	0000300310	1000002000	0001200000	0000000000	0000000100	0200000002	02000
91102	3120011023	0000300310	0000002000	0001000000	0000000000	0000000100	0100000002	02000
91103	3030011023	0000300310	1000002000	0100000000	0000000000	0000000100	0100000002	02000
91104	3030011023	0000310310	1000002000	0001100000	0000000000	0000000100	0200000002	02000
91105	3030011033	0000310310	1000002000	0001100000	0000000000	0000000100	0200000001	02000
91106	3030011023	0000300310	0000002000	0101100000	0000000000	0000000100	0200000002	02000
91107	3030011023	0000310310	0000002000	0101100000	0000000000	0000000100	0200000001	02000

V. *Kalmia latifolia*

9136	3001000023	0001200100	0000002020	0000000000	0000000020	2313000100	0133222012	00000
9137	3001000023	0001000200	0000000010	0000000000	0000000020	2313000100	0233322012	00000
9138	3001000023	0001000300	0000001000	0000000000	0000000020	3313000100	0133222013	00000
9139	3001000023	0001100300	0000001010	0000000000	0000000020	3313000100	0132322003	00000
9140	3002000023	0000000300	0000001010	0000000000	0000000000	3313000100	0132322013	00000
9141	3001000023	0001000300	0000000010	0000000000	0000000020	3313000100	0132221003	00000
9142	3001000023	0001100200	0000001000	0000000000	0000000020	3313000100	0131222012	00000
9146	3001000023	0000100200	0000001010	0000000000	0000000020	3313000100	0131221013	00000
9147	3001000013	0000000200	0000001000	0000000000	0000000010	3313000100	0131221002	00000
9150	3021000023	0000100300	0000002010	0000000000	0000000000	3313000100	0131222002	00000
9152	3001000023	0000100300	0000001020	0000000000	0000000000	3313000100	0131221003	00000
9153	3002000023	0001100300	0000001030	0000000000	0000000020	3313000100	0133222002	00000
9154	3002000033	0001000200	0000000020	0000000000	0000000000	3313000100	0133232002	00000
9155	3011000023	0001100210	0000002020	0000000000	0000000020	3313000100	0133322002	00000
9156	3001000013	0000100200	0000001000	0000000000	0000000020	3212000100	0133222002	00000
9157	3001000023	0000100200	0000001000	0000000000	0000000020	3213000100	0132221002	00000
9158	3001000023	0000100200	0000001000	0000000000	0000000020	3213000100	0132221003	00000
9159	3001000023	0001100200	0000001000	0000000000	0000000020	3313000100	0132222002	00000
9166	3001000023	0000200300	0000002010	0000000000	0000000020	3213000100	0132221002	00000
9167	3001000023	0000000200	0000002000	0000000000	0000000020	3212000100	0132222002	00000
9168	3000000033	0000200200	0000002000	0000000000	0000000020	3213000100	0131222002	00000
9169	3001000023	0000000200	0000002010	0000000000	0000000020	3213000100	0131121002	00000
9170	3002000033	0001100300	0000002000	0000000000	0000000020	3313000100	0131221002	00000
9171	3001000023	0000100300	0000002000	0000000000	0000000010	3313000100	0131121002	00000
9172	3002000023	0000000300	0000001020	0000000000	0000000020	3303000100	0133321013	00000
9173	3002000023	0001200300	0000001020	0000000000	0000000020	3213000100	0132222013	00000
9174	3002000023	0000000200	0000002020	0000000000	0000000000	3213000100	0131121002	00000
9175	3002000023	0000100300	0000002000	0000000000	0000000020	3213000100	0132221002	00000
9176	3002000023	0000100300	0000002020	0000000000	0000000000	3213000100	0132212003	00000
9178	3002000023	0000100300	0000002000	0000000000	0000000020	3213000100	0133212002	00000
9179	3001000023	0000100300	0000002000	0000000000	0000000010	3213000100	0131012002	00000
9197	3001000013	0000000100	0000001000	0000000000	0000000000	3103000100	0133321003	00000
NB784	2001000023	0000000200	0000000000	0000000000	0000000000	2112000100	0132322002	00000
NB802	2002000013	0000000100	0000000000	0000000000	0000000000	3113000100	0133212001	00000
NB809	2001000023	0000000100	0000000000	0000000000	0000000020	1103000100	0133222001	00000
NB819	2001000023	0000000200	0000000000	0000000000	0000000000	3113000100	0133223002	00000
NB861	2002000013	0000000110	0000001000	0000000000	0000000000	3213000100	0132312002	00000
NS313	3001000023	0000000100	0000001000	0000000000	0000000020	1102000100	0132122000	00000
NS336	3001000023	0000000000	0000000000	0000000000	0000000020	2113000100	0333023000	00000
NS590	3001000013	0000000200	0000000000	0000000000	0000000020	3103000100	0132123000	00000

VI. *Kalmia microphylla*

AB-001	0030001023	3202320311	3000000030	1311201300	0011100000	0000000000	0300000000	01000
AB-002	0030000023	2212320310	3000000020	1310201300	0011100000	0000000000	0303000000	01000
AB-003	0030011023	2202310311	3000100020	1310101300	0011100000	0000000000	0201000000	01000
AB-005	0010000023	2202310210	1000202010	1210100200	0010000000	0000000000	0100000000	00002
AB-006	0000000023	2202300211	0000102010	1200100200	0010000000	0000000000	0100000000	00002
BC-001	0020000013	2222300311	2000000020	1311111301	1111100000	0000000000	0303000000	01000
BC-002	0020000013	2223310311	2000000031	1311012301	1111100000	0000000000	0302000000	02000
BC-003	0020001023	2211300311	2000200030	1310211300	0011100000	0000000000	0300000000	01001
BC-004	0020000023	2202310310	2000102030	1312211300	0011100000	0000000000	0300000000	01002
BC-005	0020000023	2212310211	2000101030	1310211300	0011100000	0000000000	0300000231	01002
BC-006	0020000023	2212310311	2000101020	1310211300	0011100000	0000000000	0300000112	01002
BC-007	0010000013	2212310310	2000002020	1310211300	0011000000	0000000000	0300000221	02000
BC-008	0010000013	2212300310	2000102020	1310111301	0111000000	0020000000	0200000230	01000
BC-009	0020000013	2213200311	2000002020	1311111200	0010000000	0010000000	0302000120	01000
YT-001	0020001023	2211310210	2000202021	1310211201	1110100000	0000000000	0300000000	01000
YT-002	0020000023	2211300310	2000102021	1311211201	1111100000	0000000000	0300000000	01000
9001	0020000023	2211320311	2000202020	1311312300	0011100000	0000000000	0200000000	01000
9002	0020001013	2211320310	2000201020	1311212300	0010100000	0000000000	0300000030	01000
9003	0020001013	2211320211	2000101020	1311212301	1111200000	0000000000	0300000120	01000
9043	0020000013	2202310310	0000001020	1300001200	0010000000	0120000000	0100000231	02000
9044	0010000013	2202311211	1000002020	1300101201	0010000000	0120000001	1100000232	02000
9045	0010000013	1102210211	2000002010	1200001300	0020000000	0120000001	0100000232	02000
9046	0020000023	1102300210	1000002000	1200101200	0000000000	0230000001	0100000232	02000
9047	0020000023	1102300210	1000002000	1200101201	0010000000	0230000000	0100000222	02000
9048	0020000023	1112300311	2000102010	2201111200	0010000000	0220000001	0200000232	02000
9049	0020000023	2212300111	2000102020	2200111201	0011000000	0220000001	0300000331	02000
9050	0020000023	1112300111	1000202010	2300111301	0010000000	0230000001	0200000331	02000
9051	0020000012	1101300010	1000102010	1200101201	0010000000	0220000000	0100000221	02000
9052	0030000013	1113201210	1000001010	1100011200	0010000000	0110000000	0100000221	02000
9053	0020000013	2211300211	2000002020	1301211200	0011000000	0120000000	0100000221	02000
9054-7	0020000013	2213100311	1000002020	1311111200	0010000000	0120000000	0302000121	02000
9058	0020000013	2211300211	1000002010	2300111201	1011000000	0120000000	0200000231	02000
9059	0020000013	2212300111	1000002020	2300111201	0011000000	0120000000	0200000231	02000
9060	0010002023	2211300310	0000001020	2301211300	0011000000	0000000000	3200000000	02000
9061	0020022023	2201300210	2000201030	1311301300	0011000000	0000000000	0200000230	02000
9062	0020000023	2211300310	3000001030	2302201300	0021000000	0000000000	3200000221	02000
9063	0020011023	2211300311	3000002031	2311311300	0010100000	0000000000	2300000221	02000
9064	0020000023	2211300310	2000102030	2311211200	0010100000	0000000000	3200000221	02000
9065	0020000023	2211320310	2000101020	2311311300	0011100000	0000000000	2200000221	01002
9066	0020000023	2211310311	2000102031	2310211300	0011100000	0000000000	1300000000	01002
9067-9	0010000023	1111300310	2000102021	2310211300	0011100000	0000000000	0300000000	01002
9070	0020010023	2210310310	2000102021	2310201300	0010100000	0000000000	0300000000	00002
9071	0020000023	2210300210	2000001020	2310301300	0001100000	0000000000	0300000000	01003
9201	0030011013	2212310310	2000000030	2310212300	0011100000	0000000000	0200000330	01000
A13882	0020000023	2213320211	2000000020	2312211200	0001100000	0000000000	0100000000	02000
A30296	0030000013	2222311210	1000100020	1312211200	0010100000	0000000000	0100000000	01000
A57455	0020000013	2213301111	1000000011	1300001100	0011100000	0000000000	0213000020	02000
A78645	0020000013	2212302211	2000000010	1210210200	0010100000	0000000000	0100000000	01000
A78967	0020000023	2211320311	2000100010	1312211200	0012100000	0000000000	0100000000	02000
A79405	0020000013	2212300211	2000000010	1310211200	0011100000	0000000000	0100000000	02000
C88255	0030000013	2212301211	2000000010	1312211200	0010100000	0000000000	0100000000	02000
C252181	0030000013	2212310211	2000000020	1312211200	0011100000	0000000000	0100000000	02000
C342230	0020000023	3311302211	1000200010	2312221300	0011100000	0000000000	0200000000	01000
D135252	0020000013	2212300211	1000000010	1312221300	0011100000	0000000000	0200000000	01000
D169629	0030000013	2212311211	2000000020	1312211200	0010100000	0000000000	0100000000	02000
D401923	0020000013	2222320211	2000000020	1312211200	0010100000	0000000000	0100000000	01000
D473045	0020000013	2212200111	1000000010	1310011200	0010000000	0010000000	0100000020	02000
D473147	0030000013	2222300210	2000000020	1311211200	0010100000	0000000000	0100000000	02000
D473183	0020000013	2212300111	2000000010	1210211200	0010000000	0010000000	0100000030	01000
D473192	0030000013	2212300011	2000000010	1310111200	0010000000	0010000000	0100000030	02000
D473234	0030000013	2212300111	2000000001	1200001200	0010000000	0010000000	0100000030	01000
D473309	0030000013	2213200211	1000200010	1312011100	0010100000	0000000000	0202000030	02000
D473315	0030000013	2213300212	1000201010	1312001200	0010100000	0000000000	0203000000	02000
D473328	0030000023	3313310211	2000001010	1313012200	1110100000	0000000000	0102000120	02001
JWT708	0030000013	2212210211	2000002020	1310011201	0120100000	0000000000	0201000230	02002
NY-BG	0020000023	2202300311	2000202010	1312211100	0010100000	0000000000	0102000020	02000

VII. *Kalmia polifolia*

AB-001	2030011013	2203230211	3000200010	1210012311	0011100000	0000201100	2200000000	03000
AB-002	2030022023	3303320211	3000200010	1310011310	0011100000	0000000001	2200000000	03000
AB-003	1030000013	2203320211	3000200020	1310012310	0011000000	0000101000	2200000000	02000
AB-004	2030001023	2203320111	3000100021	2310012312	1211100000	0000112100	2200000000	03000
AB-005	2020011023	2203320311	3000200020	1310012311	1211100000	0000211202	1200000000	03000
AB-006	3020000013	2203320211	2000200021	1310012310	0011000000	0000101201	2300000000	02000
9004	2020000023	2203320210	2000202021	1311011211	0111100000	0000212201	1100000000	03000
9005	1030000023	2203310210	2000000210	2100001200	0010000000	0000211100	0000000000	01000
9006	2020001033	3303320210	2000001120	2210012312	1211100000	0000212201	1100000000	02000
9007	2020000033	3302320311	2000110120	2200002210	0010100000	0000111101	1100000000	02000
9008	2030000033	2202320211	2000201011	2200011211	1110100000	0000101101	1000000000	02000
9009	2030000023	2203310211	1000100010	1210012311	0110000000	0000211201	1200000000	02000
9010	3030011023	3303320211	2000202021	2310012311	0110100000	0000101101	1200000000	03000
9011	2020010033	3303320211	2000101021	1210002200	0010100000	0000101201	2000000000	02000
9012	2030020023	2203320210	1000201210	2310012201	0110100000	0000201100	0000000000	02000
9013	3030000033	2203320211	2000201021	1310022201	0110100000	0000201201	1200000000	03000
9014	2030001033	2203320210	2000300021	2210012211	0110100000	0000101100	0000000000	03000
9015	2020000013	2203320211	2000010021	1310012211	0111100000	0000101101	1200000000	02000
9016	1030000033	2203310211	2000200021	2310021211	0011100000	0000101100	0000000000	03000
9017	1030001023	2203320211	2000000031	1210011201	0011100000	0000111200	1200000000	02000
9018	1030011023	3303320210	1000201021	1210012211	0111000000	0000212201	0200000000	03000
9019	1030000023	2203320211	2000301021	1310012210	0011100000	0000101100	1100000000	02000
9020	2020000023	3303310210	1000100000	2210012312	0111000000	0000212201	1100000000	02000
9021	1020000013	2203320210	1000300021	0310011200	0012100000	0000000001	2100000000	02000
9023	1030001023	3303320210	2000100020	2210002211	0111100000	0000211100	1100000000	02000
9024	2030000013	2203320111	2000210021	2310012212	1111000000	0000211200	1000000000	02000
9025	2030011133	2203220210	2000210031	2310012311	0111100000	0000111201	0100000000	02000
9026	2020000023	2203310211	2000200021	1310012311	0111100000	0000211200	1100000000	02000
9027	1030000023	2203310211	2000100021	2310012311	1111100000	0000212200	1000000000	02000
9028-31	0030101123	2203320211	2000201121	1310012211	0111100000	0000111100	1100000000	02000
9032-6	0030001023	2203320211	2000101021	1310012211	1111100000	0000111101	1200000000	02000
9037	2030000023	3303320211	2000101031	1310012211	0111100000	0000211200	1200000000	02000
9038	2030000023	2203320211	2000000020	1300012210	0111100000	0000211200	1100000000	02000
9039	2030000023	2203320210	2000201010	1210012211	0111000000	0000212200	1000000000	02000
9040	2030000023	2203320211	2000001030	1300012111	0111100000	0000111100	1100000000	03000
9041	2030000023	2203310110	2000100031	1300012211	0111100000	0000111201	2200000000	02000
9042	3030001123	2203320210	2000200020	1310012210	0011100000	0000211200	2200000000	02000
9101	2030000023	1103320220	3000000031	1300012310	0121100000	0000101100	1200000000	03000
9102	2030000013	3303320211	2000101011	0300011210	0011000000	0000101100	1100000000	02000
9103	2020000013	3303320210	3000200031	1310012311	1111100000	0000101101	1200000000	03000
9104	2020000013	2203320210	2000101021	1210012310	1211000000	0000111200	0100000000	02000
9105	2030000013	2203320211	2000000021	1310022311	1011100000	0000101100	1100000000	03000
9106	2030001013	2203320111	2000310031	1310012311	0111100000	0000101100	1200000000	03000
9108	2030000013	2203320211	3000102031	1310012311	1111100000	0000101100	1200000000	03000
9110	2030001013	3303320211	2000100030	1310012310	1111100000	0000101200	0200000000	03000
9111	2030001013	2203320210	2000202031	1310012311	0111100000	0000211200	0200000000	03000
9114	0020000013	2203320211	2000001031	1310012310	1111100000	0000111100	0200000000	03000
9117	3030000023	3303330211	3000111030	1300012311	1111100000	0000211201	1300000000	03000
9118	2030000023	3303330210	1000102020	1310011211	0111000000	0000101100	1300000000	03000
9121	3030000013	0003320210	2000100010	1300002310	1111000000	0000101100	0000000000	03000
9122	1030000013	2203320211	1000200030	1300011211	0011100000	0000101100	0200000000	03000
9128	2030000013	1103320210	1000102020	1300011211	1111000000	0000101200	1200000000	03000
9134	0030000023	2203320310	1000202120	2210011111	0111100000	0000211100	0000000000	02000
9202	2030001013	2203321311	3000200030	1322012320	0011100000	0000101100	0300000000	03000
AW	3030000013	2203300010	1000000020	2300001202	0010000000	0000112200	0000000000	02000
NW-1	2030000003	2202320010	2000200020	0300001200	0010000000	0000000000	0200000000	02000
NW-2	2030000003	2202220110	2000100020	0300001200	0011100000	0000001000	1100000000	02000
PJS	2030000013	1102320011	2000100020	0200001200	0010000000	0000101100	0200000000	02000

The Flavonoid Order Adopted in Appendix 2

FLAVONE	M#
1.8-desmethyl eucalyptin (mixed with 2)	
2. 8-desmethyl sideroxylin	1
2.1 -5-O-ara**	2
3. Undetermined	3
FLAVONOL	
4. 8-desmethyl kalmiatin	4
5. Kaempferol	5
5.1 3-O-rham	6
5.2 3-O-ara	7
5.3 3-O-rut	8
6. Quercetin	9
6.1 3-O-gal (hperin)	10
6.2 3-O-gal derv	11
6.3 3-O-gal derv	12
6.4 3-O-glu	13
6.5 3-O-ara fur	14
6.6 3-O-ara pyr	15
6.7 3-O-rut	16
6.8 3-O-gal glu	17
6.9 3-O-rham ara	18
6.10 7-O-glu	19
6.11 3'-O-glu gal	20
6.12 3'-O-glu xyl	21
7.Quercetin-3-O-methyl ether	22
7.1 3'-O-xyl	23
8.Isorhamnetin	24
8.1 3-O-gal	25
8.2 3-O-ara	26
9. Quercetin-3,5,3'-tri-O-methyl ether ?	27
10. Gossypetin	28
10.1 3-O-gal	29
10.2 3-O-monogly	30
11. Myricetin	31
11.1 3-O-gal	32
11.2 3-O-glu	33
11.3 3-O-rham	34
11.4 3-O-ara pyr	35
11.5 3-O-ara fur	36
11.6 3'-O-glu	37
11.7 3'-O-xyl	38
11.8 5'-O-xyl(?)	39
12. Myricetin-3-O-methyl ether	40
12.1 3'-O-xyl	41
12.2 3'-O-glu xyl	42
Undetermined glycosides	
Ufg.1 ? gly	43
Ufg.2 7-gly	44
Ufg.3 7-gly	45

CHALCONE	M#
13. Agl#1	46
14. Agl#2	47
15. Agl#3	48
Glycosides:	
Cg.1 glu	49
Cg.2 gly	50
Cg.3 gly	51
AURONE	
16. Agl#1	52
16.1 rham(?)	53
16.2 glu	54
17. Agl#2	55
Glycosides:	
17.1 gly(1)	56
17.2 gly(2)	57
17.3 gly(3)	58
DIHYDROFLAVONOL	
18. Taxifolin (dihydroquercetin)	59
18.1 3-O-glu	60
18.2 3-O-xyl	61
CATECHIN	
19. D(+)-catechin	62
DIHYDROCHALCONE	
20. Phloretin	63
20.1 2'-O-glu (phloridzin)	64
20.2 2'-O-glu monoacet	65
21. 3-hydroxy phloretin	66
21.1 2'-O-glu	67
22. Asebogenin	68
22.1 2'-O-glu (asebotin)	69
22.2 2'(?)-O-gal xyl	70
23. Asebogenin-C-methyl ether (?) (new?)	71
FLAVANONE	
24. #1 (gly)	72
25. #2	
25.1 gly(1)	73
25.2 gly(2)	74
26. #3 agl.	75

Note: For complete flavonoid names, see Table 6.

Appendix 3. The Flavonoid Distributions in *Kalmia*

Notes:

1. *Lat = K. latifolia; ang = K. angustifolia; cun = K. cuneata; eri = K. ericoides; hir = K. hirsuta; mic = K. microphylla; pol = K. polifolia.*
2. Number in parentheses is the number of populations scanned for flavonoids.
3. Refer to Table 6 for the flavonoid identity.

I. The Distributions of All Flavonoids

A. Number of Populations Having the Flavonoid

Flavonoid	*lat* (40)	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2	40	30	0	9	25	0	54
2.1	0	10	0	2	2	0	0
3	2	26	3	3	25	64	58
4	39	0	0	0	0	0	0
5	0	0	1	0	1	0	1
5.1	0	0	4	4	25	5	8
5.2	0	0	0	6	25	10	18
5.3	0	0	4	5	0	0	3
6	40	45	5	9	25	66	56
6.1	40	45	5	9	25	66	58
6.2	0	0	0	6	0	66	57
6.3	0	0	0	0	0	66	57
6.4	0	0	0	0	0	53	0
6.5	12	45	5	6	0	64	58
6.6	21	45	5	9	25	66	58
6.7	0	37	5	1	4	28	57
6.8	0	0	0	0	0	8	1
6.9	39	43	5	9	25	65	55
6.10	2	38	5	9	25	66	58
6.11	0	0	5	2	2	42	34
6.12	0	0	0	0	22	63	58
7	0	15	0	0	0	0	0
7.1	0	26	4	0	0	0	0
8	0	0	0	0	0	0	0
8.1	0	0	0	0	0	28	48
8.2	0	0	0	0	0	0	6
9	31	36	0	1	25	41	23
10	0	0	0	0	0	0	6
10.1	17	35	0	5	1	63	57
10.2	0	0	0	0	0	8	31
11	0	0	0	0	5	66	53
11.1	0	0	0	0	16	66	58

I. A continued

Flavonoid	*lat*	*ang*	*cun*	*eri*	*hir*	*mic*	*pol*
11.2	0	0	0	0	0	47	42
11.3	0	0	0	0	24	32	2
11.4	0	0	0	0	19	55	0
11.5	0	0	0	0	0	48	49
11.6	0	0	0	0	0	63	58
11.7	0	0	0	0	0	66	58
11.8	0	0	0	0	0	0	48
12	0	0	0	0	0	14	38
12.1	0	3	0	0	0	7	16
12.2	0	0	0	0	0	8	38
Ufg.1	0	40	2	0	0	64	58
Ufg.2	0	0	0	0	0	33	46
Ufg.3	0	0	3	9	3	40	42
13	0	15	0	0	0	0	0
14	0	1	0	0	0	0	0
15	0	1	0	0	0	0	0
Cg.1	29	35	0	0	0	0	0
Cg.2	0	30	0	0	0	0	0
Cg.3	40	37	0	0	0	0	0
16	40	9	0	0	0	14	0
16.1	35	22	0	0	0	20	0
16.2	40	0	0	0	0	0	0
17	0	0	1	0	5	0	54
17.1	0	0	0	0	0	0	29
17.2	0	0	0	0	0	0	55
17.3	40	30	2	0	25	0	53
18	0	0	0	0	0	0	0
18.1	0	0	0	0	0	6	20
18.2	0	0	0	0	0	7	41
19	40	45	5	9	25	66	46
20	40	0	0	0	0	1	0
20.1	40	0	0	0	0	12	0
20.2	38	0	0	0	0	0	0
21	40	0	0	0	0	0	0
21.1	40	0	0	0	0	0	0
22	?	30	0	5	0	28	0
22.1	8	31	0	0	0	36	0
22.2	37	35	0	9	25	21	0
23	?	?	0	?	?	?	0
24	0	38	5	6	25	63	58
25	0	0	0	0	0	0	0
25.1	0	39	0	0	0	0	0
25.2	0	44	0	0	0	0	0
26	0	4	0	8	0	13	0
Total Flavonoids	27	34	19	24	27	47	46

I. B Percentage of Populations Having the Flavonoid

Flavonoid	*lat* (40)	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2	100	67	0	100	100	0	93
2.1	0	22	0	22	8	0	0
3	5	58	60	33	100	98	100
4	98	0	0	0	0	0	0
5	0	0	20	0	4	0	2
5.1	0	0	80	44	100	8	14
5.2	0	0	0	67	100	15	31
5.3	0	0	80	56	0	0	5
6	100	100	100	100	100	100	97
6.1	100	100	100	100	100	100	100
6.2	0	0	0	67	0	100	98
6.3	0	0	0	0	0	100	98
6.4	0	0	0	0	0	80	0
6.5	30	100	100	67	0	97	100
6.6	53	100	100	100	100	100	100
6.7	0	82	100	11	16	42	98
6.8	0	0	0	0	0	12	2
6.9	96	98	100	100	100	98	95
6.10	5	84	100	100	100	100	100
6.11	0	0	100	22	8	64	59
6.12	0	0	0	0	88	95	100
7	0	33	0	0	0	0	0
7.1	0	58	80	0	0	0	0
8	0	0	0	0	0	0	0
8.1	0	0	0	0	0	42	80
8.2	0	0	0	0	0	0	10
9	78	80	0	11	100	62	40
10	0	0	0	0	0	0	10
10.1	43	78	0	65	4	95	98
10.2	0	0	0	0	0	12	53
11	0	0	0	0	20	100	98
11.1	0	0	0	0	64	100	100
11.2	0	0	0	0	0	71	72
11.3	0	0	0	0	96	48	3
11.4	0	0	0	0	76	83	0
11.5	0	0	0	0	0	73	84
11.6	0	0	0	0	0	95	100
11.7	0	0	0	0	0	100	100
11.8	0	0	0	0	0	0	83
12	0	0	0	0	0	21	66
12.1	0	7	0	0	0	11	28
12.2	0	0	0	0	0	12	66
Ufg.1	0	89	40	0	0	97	100
Ufg.2	0	0	0	0	0	50	79
Ufg.3	0	0	60	100	12	60	72

I B Continued

Flavonoid	*lat*	*ang*	*cun*	*eri*	*hir*	*mic*	*pol*
13	0	33	0	0	0	0	0
14	0	2	0	0	0	0	0
15	0	2	0	0	0	0	0
Cg.1	73	78	0	0	0	0	0
Cg.2	0	67	0	0	0	0	0
Cg.3	100	82	0	0	0	0	0
16	100	20	0	0	0	21	0
16.1	88	49	0	0	0	30	0
16.2	100	0	0	0	0	0	0
17	0	0	20	0	20	0	93
17.1	0	0	0	0	0	0	50
17.2	0	0	0	0	0	0	95
17.3	100	67	40	0	100	0	91
18	0	0	0	0	0	0	0
18.1	0	0	0	0	0	9	34
18.2	0	0	0	0	0	11	71
19	100	100	100	100	100	100	79
20	100	0	0	0	0	2	0
20.1	100	0	0	0	0	18	0
20.2	95	0	0	0	0	0	0
21	100	0	0	0	0	0	0
21.1	100	0	0	0	0	0	0
22	?	67	0	56	0	42	0
22.1	20	69	0	0	0	55	0
22.2	93	76	0	100	100	32	0
23	?	?	0	?	?	?	0
24	0	84	100	67	100	95	100
25	0	0	0	0	0	0	0
25.1	0	87	0	0	0	0	0
25.2	0	98	0	0	0	0	0
26	0	9	0	89	0	20	0
Total Flavonoids	27	34	19	24	27	47	46

II Distributions of Aglycones

A Number of Populations Having the Flavonoid

Flavonoid	*lat* (40)	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2	40	31	0	9	25	0	54
3	2	26	3	3	25	65	58
4	39	0	0	0	0	0	0
5	0	0	5	7	25	10	21
6	40	45	5	9	25	66	58
7	0	26	4	0	0	0	0
8	0	0	0	0	0	28	49
9	31	36	0	1	25	41	23
10	17	36	0	5	1	64	57
11	0	0	0	0	25	66	58
12	0	3	0	0	0	15	44
13	40	40	0	0	0	0	0
14	40	40	0	0	0	0	0
15	?	?	0	0	0	0	0
16	40	22	0	0	0	20	0
17	40	30	2	0	25	0	55
18	0	0	0	0	0	12	43
19	40	45	5	9	25	66	46
20	40	0	0	0	0	12	0
21	40	0	0	0	0	0	0
22	40	45	0	9	25	37	0
23	?	?	0	?	?	?	0
24	0	38	5	6	25	63	58
25	0	44	0	0	0	0	0
26	0	4	0	8	0	13	0
Total Aglycones	16	18	7	11	12	16	13

B Percentage of Populations having the Flavonoid

Flavonoid	*lat* (40)	*ang* (45)	*cun* (5)	*eri* (9)	*hir* (25)	*mic* (66)	*pol* (58)
1&2	100	69	0	100	100	0	93
3	5	58	60	33	100	98	100
4	98	0	0	0	0	0	0
5	0	0	100	78	100	15	36
6	100	100	100	100	100	100	100
7	0	58	80	0	0	0	0
8	0	0	0	0	0	42	84
9	78	80	0	11	100	62	40
10	43	80	0	56	4	97	98
11	0	0	0	0	100	100	100
12	0	7	0	0	0	23	76
13	100	100	0	0	0	0	0
14	100	100	0	0	0	0	0
15	?	?	0	0	0	0	0
16	100	49	0	0	0	30	0
17	100	67	40	0	100	0	95
18	0	0	0	0	0	18	74
19	100	100	100	100	100	100	79
20	100	0	0	0	0	18	0
21	100	0	0	0	0	0	0
22	100	100	0	100	100	56	0
23	?	?	0	?	?	?	0
24	0	84	100	67	100	95	100
25	0	98	0	0	0	0	0
26	0	9	0	89	0	20	0
Total Aglycones	16	18	7	11	12	16	13

Appendix 4. *Kalmia* Flavonoid Order on 2D PC (Fig. 3)

PC Spot#[a]	Series #[b]	Spot code[c]	RFs[d]	
			BAW	AW
1	11.6	Kp28	.13	.02
2	11.8	Kp36b(1)	.18	.02
3	11.7	H1	.21	.03
4	10.	B15	.31	.03
5	11.	19-32(2)	.39	.02
6	17.1	Kp26(1)	.48	.04
7	6.	Y1	.61	.02
8	8.	19-32(1)	.65	.02
9	17.	Y2	.73	.02
10	16.	Kp38(1)	.75	.04
11	5.	Y3	.83	.02
12	1.	Ch11	.91	.02
13	2.	Ch11(1)	.91	.02
14	23.	P2	.94	0
15	Ufg.2	47-71(1)(1)	.10	.08
16	6.10	C7(1)	.19	.08
17	Cg.2	G5(1)	.23	.08
18	6.11	B10-11	.29	.07
19	12.2	Kp15	.30	.11
20	17.2	Kp14	.29	.08
21	16.2	D1(1)	.30	.08
22	12.1	Kp21	.34	.08
23	6.12	F2	.49	.05
24	12.	Kp37	.66	.06
25	13.	Ch13(Kang)	.78	.05
26	7.	B12-13	.84	.10
27	4.	Ch11(2)	.90	.08
28	16.1	A1(1)	.39	.13
29	Ufg.3	Flanol-7	.43	.12
30	17.3	Kp26(2)	.28	.14
31	2.1	A1(2)	.50	.14
32	7.1	C6(b)	.60	.16
33	14.	Ch15(Kang)	.80	.13
34	21.	B14(1)	.83	.15
35	11.5	Kp22	.33	.19
36	6.4	J1	.34	.20
37	Cg.3	G5(2)	.40	.19
38	15.	Ch16(Kang)	.90	.25
39	20.	A4(1)	.91	.22
40	22.	P1	.93	.22
41	11.2	Kp23	.23	.24
42	10.2	Kp16	.20	.28

Appendix 4 continued

43	11.1	D3(1)	.33	.29
44	6.2	J2	.36	.32
45	Cg.1	G5(3)	.40	.34
46	11.4	Kh100	.52	.25
47	6.5	C7(2)	.54	.27
48	8.2	Kp17(D3b)	.58	.30
49	6.3	D4(1)	.44	.33
50	6.1	B2	.54	.36
51	11.3	Kp24(2)	.54	.40
52	6.6	D4(2)	.71	.33
53	8.1	G8	.70	.39
54	5.2	Kp24(1)	.76	.38
55	10.1	C1-3(2)	.31	.35
56	6.8	B1(1)	.32	.41
57	21.1	B1(2)(2)	.49	.49
58	6.9	B6(1)	.69	.49
59	5.1	B6(2)	.76	.50
60	19.	10(1)	.35	.53
61	6.7	C1-3(1)	.53	.52
62	20.1	A4(2)	.68	.56
63	25.1	KaA	.80	.54
64	Ufg.1	6(1)	.34	.56
65	5.3	8(2)	.44	.57
66	18.	Kp7(1)	.76	.52
67	9.	6(3)	.81	.60
68	25.2	KaB(1)	.50	.61
69	22.1	EA16(Kang)	.78	.63
70	18.2	Kp9(2)	.57	.69
71	3.	Kp5(2)	.68	.75
72	24.	4(4) (H14)	.70	.77
73	20.2	Klat	.80	.75
74	26.	Ch16	.86	.70
75	18.1	Kp7(2)	.48	.76
76	22.2	4(3)	.57	.79

Notes:

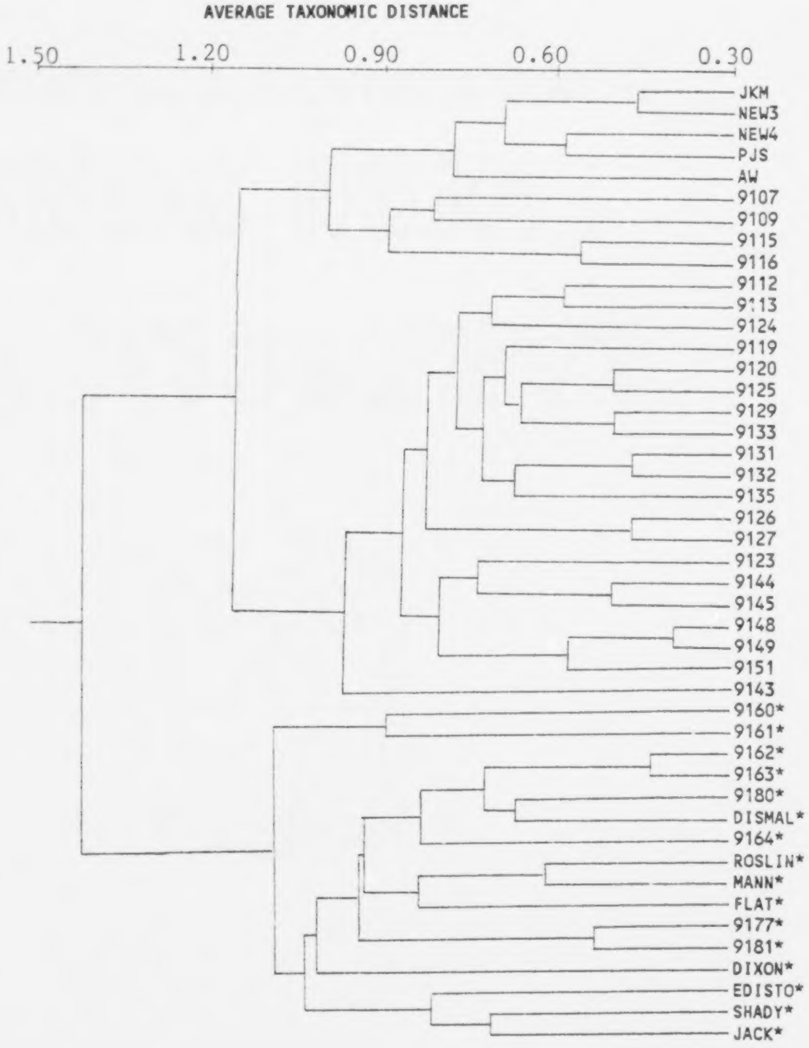
a. Spot # corresponds to Figure 3.

b. Series # corresponds to Table 6.

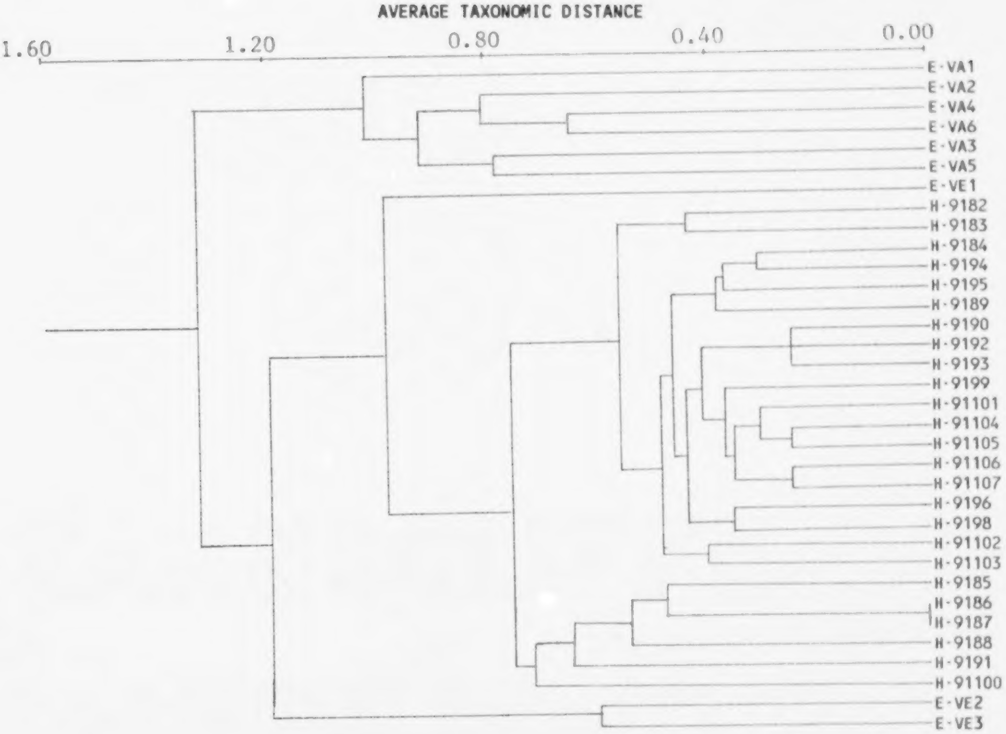
c. Spot Code is the originally assigned code.

d. Rfs are the same as in Table 7.

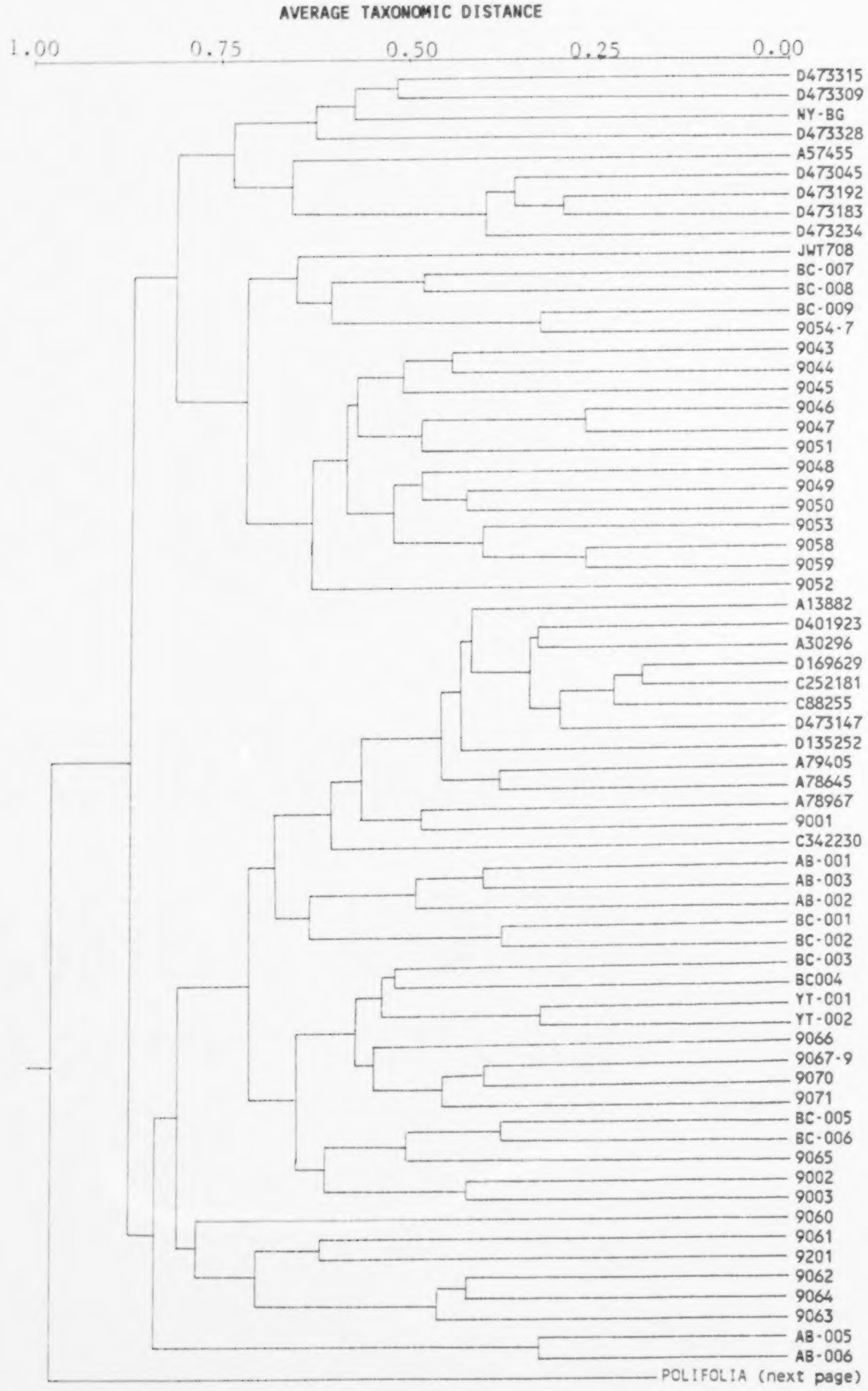
Appendix 5. Phenograms Generated in Analyses 1-4.

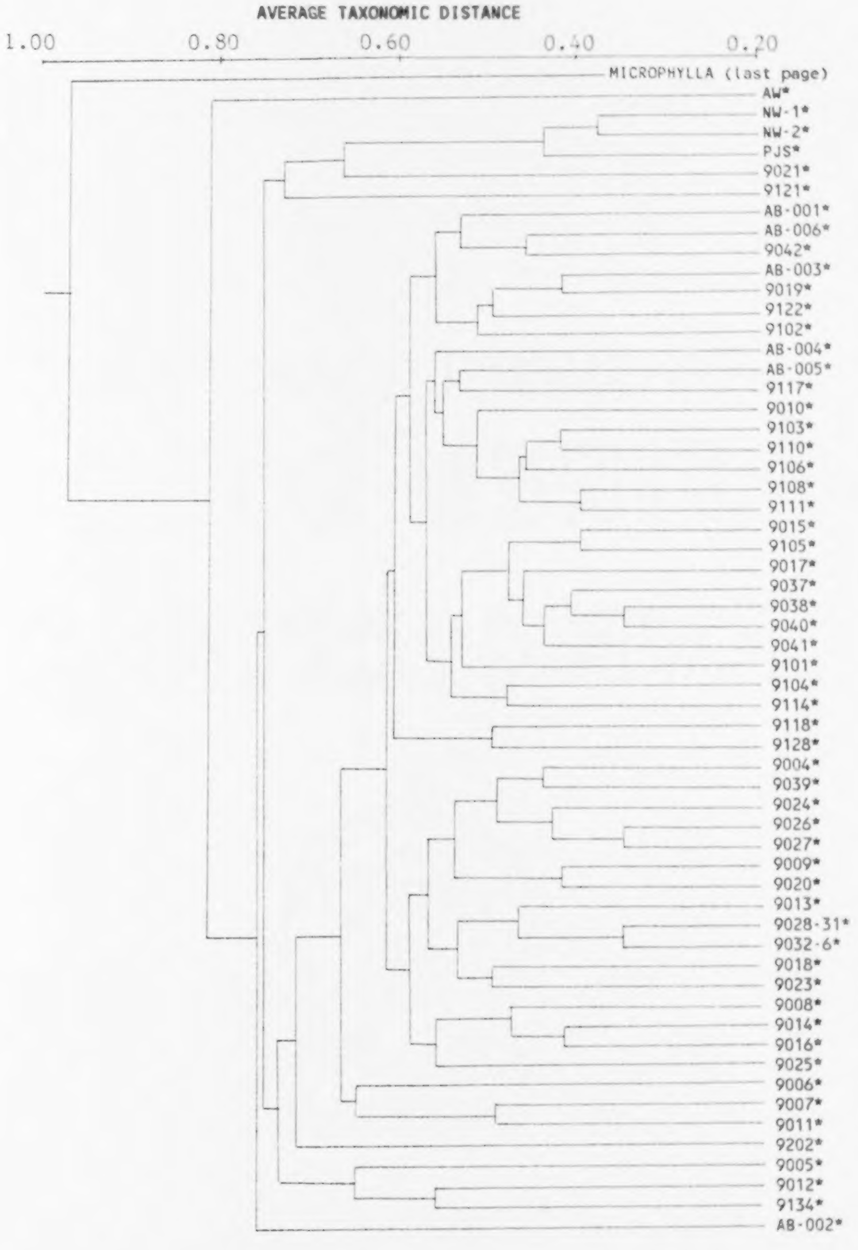


A. Cluster analysis of *Kalmia angustifolia* var. *angustifolia* (without *) and var. *carolina* (with *) populations based on flavonoid characters (Appendix 2).

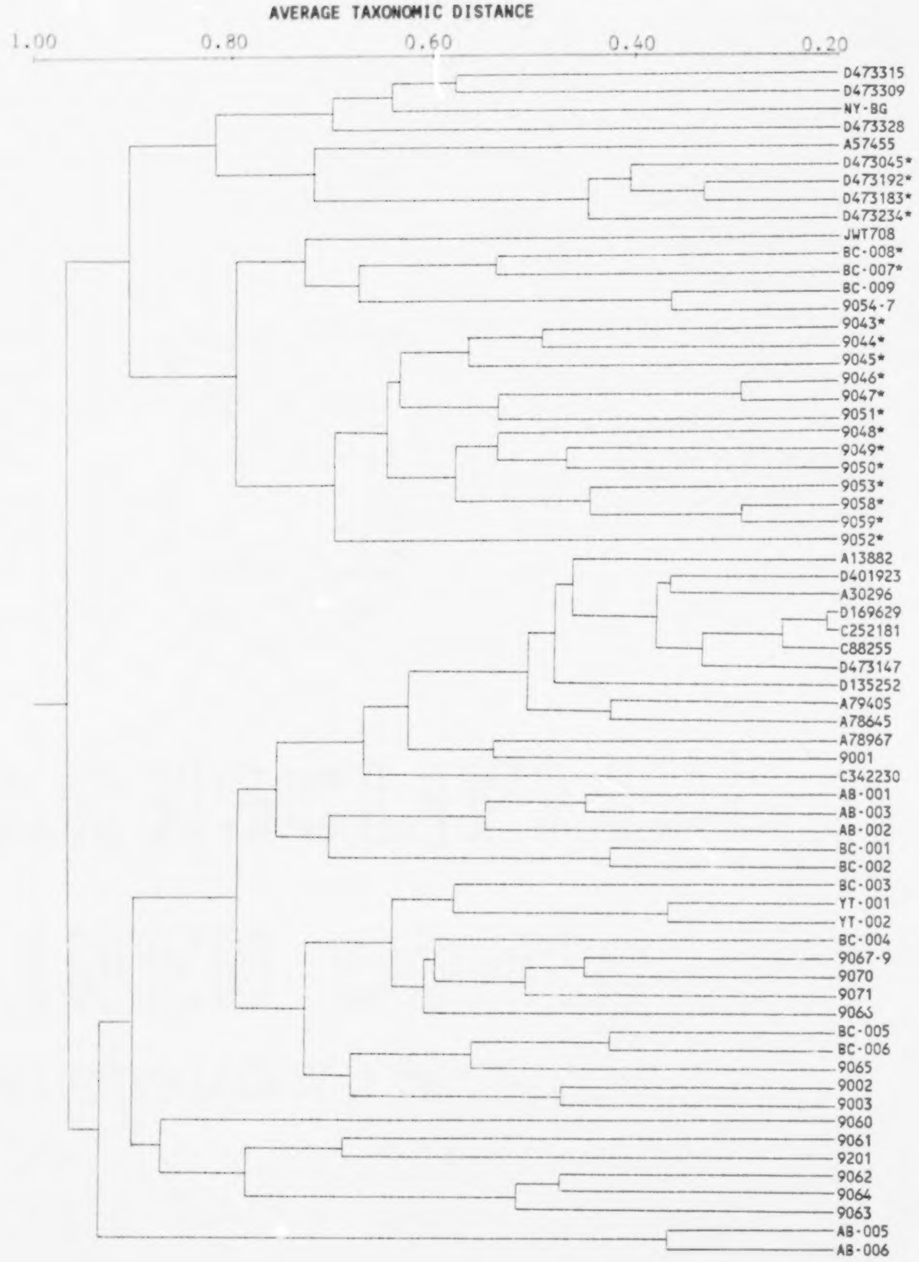

AVERAGE TAXONOMIC DISTANCE
1.60
1.20
0.80
0.40
0.00
E-VA1
E-VA2
E-VA4
E-VA6
E-VA3
E-VA5
E-VE1
H-9182
H-9183
H-9184
H-9194
H-9195
H-9189
H-9190
H-9192
H-9193
H-9199
H-91101
H-91104
H-91105
H-91106
H-91107
H-9196
H-9198
H-91102
H-91103
H-9185
H-9186
H-9187
H-9188
H-9191
H-91100
E-VE2
E-VE3

B. Cluster analysis of *Kalmia ericoides* (E) and *K. hirsuta* (H) populations based on flavonoid characters (Appendix 2).


AVERAGE TAXONOMIC DISTANCE
1.00
0.75
0.50
0.25
0.00
D473315
D473309
NY-BG
D473328
A57455
D473045
D473192
D473183
D473234
JWT708
BC-007
BC-008
BC-009
9054-7
9043
9044
9045
9046
9047
9051
9048
9049
9050
9053
9058
9059
9052
A13882
D401923
A30296
D169629
C252181
C88255
D473147
D135252
A79405
A78645
A78967
9001
C342230
AB-001
AB-003
AB-002
BC-001
BC-002
BC-003
BC004
YT-001
YT-002
9066
9067-9
9070
9071
BC-005
BC-006
9065
9002
9003
9060
9061
9201
9062
9064
9063
AB-005
AB-006
POLIFOLIA (next page)



C. Cluster analysis of *Kalmia polifolia* (with *) and *K. microphylla* (without *) populations based on flavonoid characters (Appendix 2).



D. Cluster analysis of *Kalmia microphylla* entity *microphylla* (without *) and entity *occidentalis* (with *) populations based on flavonoid characters (Appendix 2).